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THE SOCIETY FOR THE STUDY OF EVOLUTION

Vol. XV MARCH, 1961 No. 1

STUDIES ON NATURAL POPULATIONS OF *DROSOPHILA*.

I. HEAT RESISTANCE AND GEOGRAPHICAL VARIATION IN *DROSOPHILA MELANOGASTER* AND *D. SIMULANS*

A. O. Tantawy and G. S. Mallah

Faculty of Agriculture, University of Alexandria, Alexandria, Egypt, U.A.R.

Received January 8, 1960

Under laboratory conditions quantitative characters in *Drosophila*, such as body size or fecundity, are very sensitive to environmental changes, e.g., temperature fluctuations or changes in quality or quantity of food. In nature, the same situation is found where changes in annual temperature or humidity affect the type of flora as well as the size of *Drosophila* fauna.

It is well known that there is a correlation between some quantitative characters and the geographical distribution of animals. Thus, the pioneer work of Timofeeff-Ressovsky (1933) showed that strains of *Drosophila funebris* and *Drosophila melanogaster* derived from different geographical regions react differently to temperature. Studies on the morphology of wild populations as those reported by Dobzhansky (1937), Reed and Reed (1947) on *Drosophila pseudoobscura* and *Drosophila persimilis*, Stalker and Carson (1947, 1948 and 1949) on *Drosophila robusta*, Prevosti (1955) on *Drosophila subobscura*, demonstrated that wing length and other traits decrease in size with geographical distribution from north to south.

The early work of Dobzhansky and his collaborators showed that natural populations of *Drosophila pseudoobscura* in different geographical localities differed in the frequency of various inversions in the third chromosome. Further work by Dobzhansky revealed that within one locality, populations of *Drosophila pseudoobscura* exhibited seasonal variations in respect to the frequency of different inversions.

Laboratory investigations designed to test the reaction of various gene arrangements to different temperature conditions have been carried out by Dobzhansky in a series of papers on *Drosophila pseudoobscura*, Kalmus (1945) on *Drosophila melanogaster*, Dubinin and Tiniakov (1945) on *Drosophila funebris*, Moos (1955) and others on *Drosophila pseudoobscura*, and Spiess (1958) on *Drosophila persimilis*. They all found that various genotypes react differently to various temperatures.

The present study, the first of a projected series dealing with natural populations of *Drosophila* in the Middle East and surrounding areas, was designed to test an hypothesis concerning the nature of developmental homeostasis. The hypothesis to be tested can be expressed as follows: progeny

FIG. 1. Different geographical regions from which populations of *Drosophila melanogaster* and *Drosophila simulans* were captured.

of euryokous populations (i.e., populations that have a wide tolerance for various environmental factors) are better able to withstand the upper and lower limits of experimental laboratory conditions than progeny of stenokous populations.

TECHNICAL PROCEDURE

Collecting technique. All collections of *Drosophila* in the present investigation and in the future, have been and will be carried out by exposing cans measuring 6×8 in., each containing one pound of ripe bananas which was mashed, autoclaved, and then inoculated with a suspension of baker's yeast. At the time of collection, i.e., in the early morning and late afternoon, Dobzhansky and Epling (1944), about a dozen of these cans were placed on the ground in the shade of trees to attract the flies. The *Drosophila* were collected with the aid of collecting nets and were then transferred into vials containing cornmeal-molasses-agar medium.

In the laboratory the flies were etherized. Males of *Drosophila melanogaster* and *Drosophila simulans* were classified as to species by examining the genitalia. Females were placed in individual culture bottles and classified by examination of their male progeny.

Localities. Natural populations of *Drosophila melanogaster* and *Drosophila simulans* were sampled from several localities, as shown in figure 1, one each from Lebanon (Safa Valley, 3,500 ft altitude) Uganda (Namulonge, 3,775 ft altitude) and three populations from Egypt (approximately at sea level). The Egyptian populations were captured from: the University of Alexandria Farm, Alexandria; Wadi-El-Natroon, an isolated desert area halfway between Alexandria and Cairo (92 km southwest of Cairo); Luxor, about 550 km south of Cairo. *Drosophila melanogaster* as well as *Drosophila simulans* were found in all these localities except Luxor, where only *Drosophila melanogaster* was found. However a *simulans* population from Beni-Swef, about 112 km south of Cairo, was substituted for this one. These localities are designated as: LB, UG, UF, WD, LX, and BS, respectively.

Most of the collecting was done during July and August in 1956, by placing the cans under grape vines, fig, or palm trees. Dobzhansky et al. (1957) did a preliminary survey collection of the *Drosophila* fauna in

TABLE 1. *Monthly averages of percentages of humidity and temperature in different geographical regions in 1956*

Locality	Humidity %	Temperature °C
LB	60.21 ± 8.91	16.15 ± 7.38
UF	69.17 ± 7.02	20.04 ± 6.35
WD	63.66 ± 12.52	21.55 ± 6.95
BS	54.83 ± 15.24	21.90 ± 7.30
LX*	29.12 ± 14.05	25.49 ± 9.52
UG	72.94 ± 2.95	27.34 ± 1.34

* % humidity and temperature were not recorded from September to December.

Egypt and obtained the frequency distribution of adults of *Drosophila melanogaster* and *Drosophila simulans* captured from the above mentioned regions as well as other localities in Egypt. Average percentages of humidity and temperatures recorded in 1956 for all localities are presented in table 1, indicating that the Uganda locality shows the highest percentage of humidity and temperature which are constant through the year, and that the Lebanon locality is the coldest, with wider fluctuations.

Experimental. Ten captured fertilized females each of *Drosophila melanogaster* and of *Drosophila simulans* were chosen at random from each locality and placed in separate culture bottles for two days, and then transferred into fresh bottles every other day for a week in order to establish the original foundation populations. At every generation, the offspring of the ten females from each locality were intercrossed to obtain ten new bottles. In other words, males from the first bottle were intercrossed with virgin females of the second bottle, males from the second bottle with females of the third bottle, and so on to produce the first and second new bottles, respectively. Such a procedure was made to obtain the first nine bottles. The tenth new bottle was obtained by intercrossing males of the first bottle with virgin females of the tenth bottle. Progeny of the first generations of these females were not used in order to avoid any possible influence of the original environmental conditions in which females had survived.

The five different populations of *Drosophila melanogaster* and of *Drosophila simulans* were exposed to the following temperatures: 10°, 15°, 18°, 22°, 25°, 28°, 30°, and 31° C. Populations of *Drosophila melanogaster* were examined also at 31.5° C and those of *Drosophila simulans* at 30.5° C (the upper limits of temperature at which progeny can be obtained in these species). These temperatures were held constant to within 0.1° C.

Within a given temperature and locality virgin females from each of the bottles were intercrossed with males from other bottles to maintain the foundation stock as heterozygous as possible. Samples of flies were taken at random from each bottle (20 pairs) and were placed in oviposition bottles; thus one hundred oviposition bottles were used for all the populations at a given temperature. Eggs were collected from these bottles at a known temperature and cultured at the same temperature.

From each of the oviposition bottles samples of eggs were obtained and cultured in five food vials. To prevent competition in the larval stage not more than seventy eggs were introduced into each vial which contained the normal food culture. Collection and culturing of eggs were carried out on four successive days and after emergence adults were counted and classified as to sex.

From the populations emerging from each of the two vials during the first two days, ten males and ten females were obtained at random on each day, in order to measure wing and thorax length. Thus a total of 400 males and females from each locality in each temperature were examined. The total number of flies emerging from all vials on the four days was used to get an estimate of the percentage of emergence and sex-ratio in the progeny.

Measurements of wing and thorax length were obtained by the method described by Robertson and Reeve (1952) and used by the senior author as described in previous publications, Tantawy (1959). At a given temperature, all populations were treated at the same time in the same manner and to minimize environmental fluctuations the methods recommended by Robertson and Reeve were used.

Results and Discussion

Wing and thorax length. It was known from the work of Mellanby (1954) that some insects can become acclimatized to changes in temperature. Smith (1957) found that in individuals of *Drosophila subobscura* acclimatization takes place and depends on whether animals are homozygous or heterozygous, the latter showing more acclimatization.

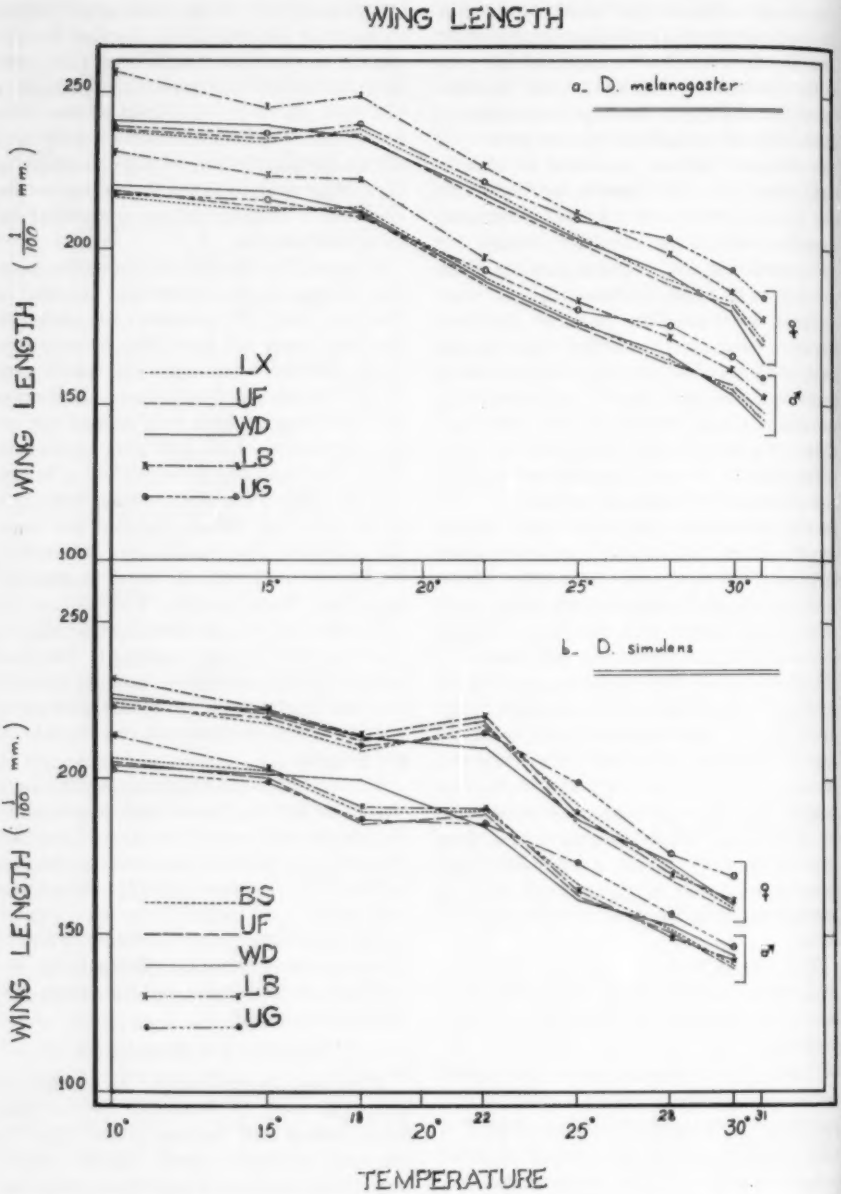


FIG. 2.: Wing length in *Drosophila melanogaster* and *Drosophila simulans* at various temperatures. Units of measurement are 1/100 mm.

Our results secured from the present experiment on the effects of various degrees of temperature on body size, i.e., wing and thorax length, in *Drosophila melanogaster* and *Drosophila simulans* are presented in figure 2 a and b for both species, respectively. Results obtained for thorax length are not given since they show a similar pattern of behavior as that obtained in the wing length.

The results as presented in figure 2 a and b indicate clearly that *Drosophila melanogaster* is significantly larger in wing length at any given temperature than is *Drosophila simulans*, and in both species the females are larger than the males. Various degrees of temperature show highly significant effects on body size; wing length is longer at the lower temperatures and decreases gradually with the increase of temperature. The average percentage of decrease, for both sexes in all populations of *Drosophila melanogaster*, from the lowest to the highest degrees, is 31.03 per cent and 18.66 per cent for wing and thorax length, respectively, and 31.79 per cent and 22.89 per cent in *Drosophila simulans* for both dimensions, respectively. Such results indicate that although *Drosophila melanogaster* is bigger in size than *Drosophila simulans*, both species were affected similarly by temperature changes, especially in regard to wing length. Such a phenomenon of changing wing length with various degrees of temperature are in agreement with the results of Stalker and Carson (1947) working on *Drosophila robusta* and Pantellouris (1957) on *Drosophila melanogaster*.

Considering the different populations from the various geographical regions, the results indicate that in both species populations from Lebanon are larger in wing length than other populations, at almost every temperature. Such a population is morphologically larger than that from Uganda where the lower temperature prevails, but the situation is reversed at the higher temperatures, where UG populations show superiority in size to all other populations. Other populations captured from Egypt do not show any significant differences between them and showed almost the same size as UG populations, except at the higher temperatures where the latter ones show longer wing length. These results will be discussed later.

Thorax length of all populations behaved almost in the same manner as wing length and figure 3 a and b for *Drosophila melanogaster* and *Drosophila simulans* shows a highly positive correlation between the two measurements. The results are presented as log of wing plotted against log of thorax which indicate also that wing length is affected more than thorax length, particularly at the extreme temperatures. Such a point can be illustrated more clearly when measurements for both dimensions are expressed as a ratio of wing/thorax length. The results for wing/thorax ratio in *Drosophila melanogaster* and *D. simulans* indicate that with an increasingly cold climate, wing length is longer relative to thorax length than it is at higher temperatures, a fact which agrees fairly well with the findings of Stalker and Carson (1947) and Pantellouris (1957). It has also been shown by Reeve and Robertson (1953) that changes of temperature during the pupal stage may have profound effects on wing length but not on thorax length.

Phenotypic variance. Phenotypic variance of wing length is expressed as the coefficient of variation and the results are presented in figure 4 a and b for *Drosophila melanogaster* and *D. simulans*.

The results as presented in figure 4 indicate that temperature has a highly significant effect on variability of wing length in all populations studied. Such variation is high at the two extremes of the temperature; higher temperatures show more effects on phenotypic variation than lower or intermediate ones. The smallest coefficients of variation appear when flies were exposed to intermediate temperatures. The results also indicate that UG populations are the highest in phenotypic variance at almost every temperature, but are the lowest at the highest temperatures. LB populations show more

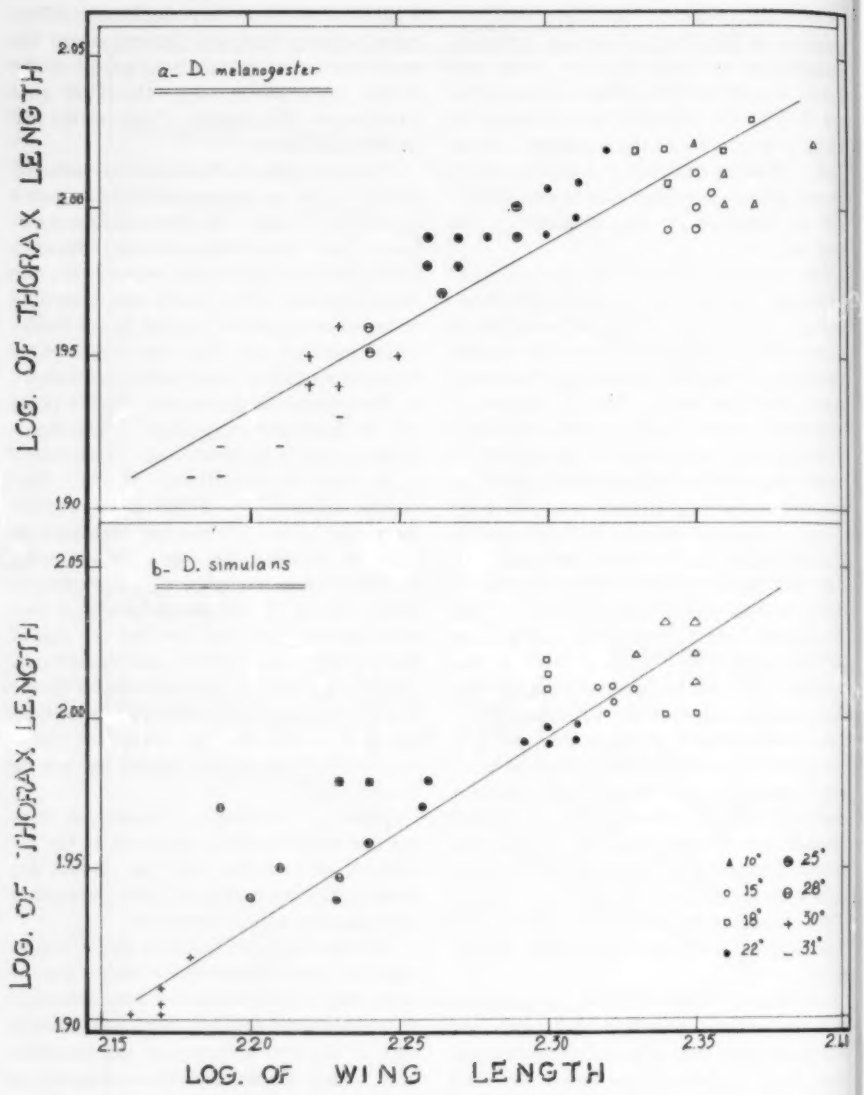


FIG. 3. Log of wing length plotted against log of thorax length in all populations of *Drosophila melanogaster* and *Drosophila simulans*.

uniformity in wing length than other populations but become the most variable at the highest temperature.

Such differences in phenotypic variance will be discussed later, but it would be of great interest to know whether the variance is a reflection of different responses of similar genotypes, or whether it is a reflection of

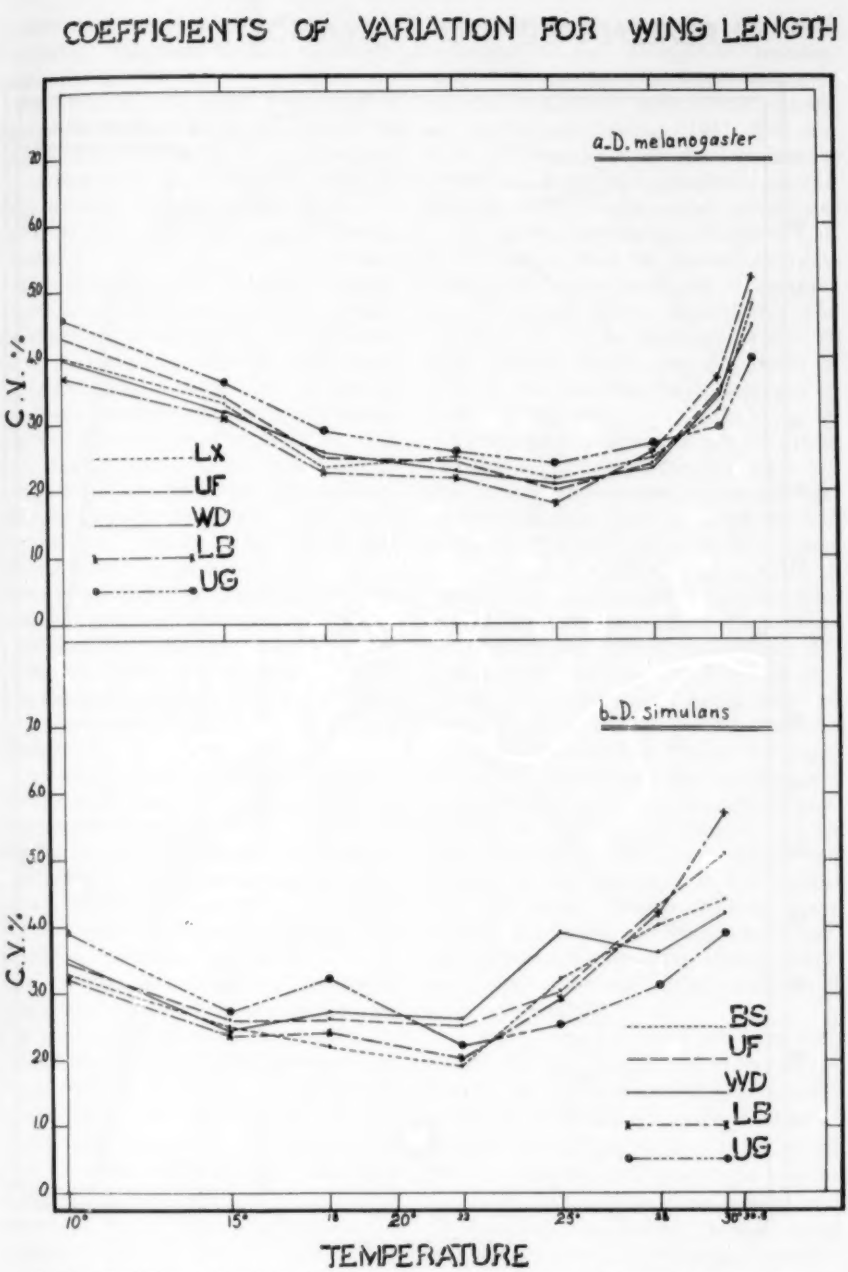


FIG. 4. Coefficients of variation for wing length of all populations of *Drosophila* in respect to different degrees of temperature.

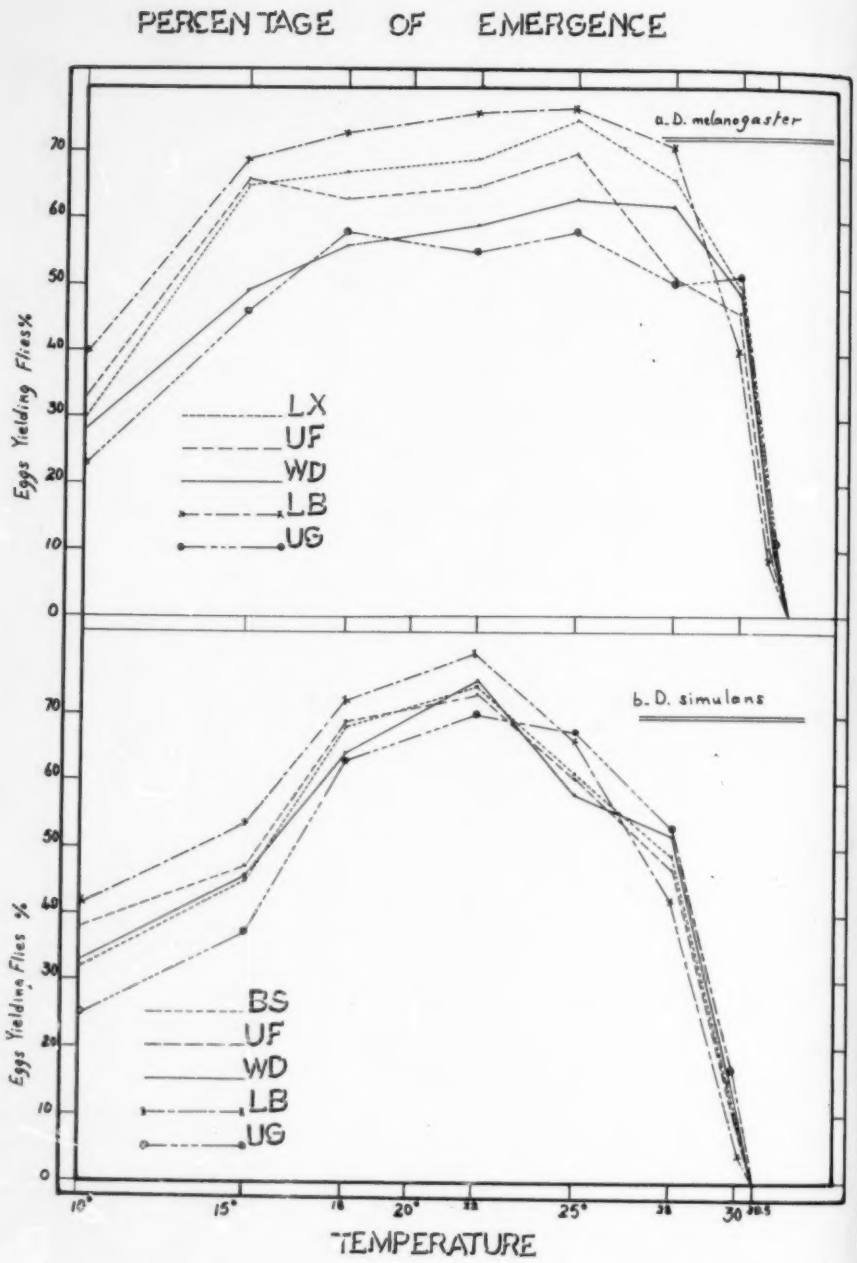


FIG. 5. Percentage of emergence in all populations of *Drosophila*.

a wider range of genotype within a given population. This point we hope to investigate in the near future.

Percentage of emergence. Percentage of emergence is measured by the number of adult flies that hatched from a certain number of eggs cultured in food vials. The results obtained are presented in figure 5 a and b for *Drosophila melanogaster* and *D. simulans*.

The results as shown in figure 5 demonstrate that different temperatures have various effects on the percentage of emergence. In all the populations studied the percentage of emergence is about 25–40 per cent at the lowest temperature, increasing gradually with the increase of temperature. The maximum percentage of emergence can be seen at 25° C, i.e., 58–76 per cent in *Drosophila melanogaster* and at 22° C, i.e., 69–79 per cent in *D. simulans*, which shows that optimal conditions for both species may be different. At higher temperatures, the percentage of emergence decreases gradually to 8 per cent and 5 per cent in both species. Complete lethality of pupae occurs at 31.5° C in *Drosophila melanogaster* and 30.5° C in *D. simulans*, thus showing a temperature difference between these sibling species.

Populations from the extreme north and extreme south end of the range differ in their per cent emergence in the same way as they differ in wing length. Populations from LB show higher percentage of emergence at almost every temperature, except that at highest temperatures where UG populations show the best viability.

If we plot percentage of emergence against the coefficients of variation for wing length the results demonstrate a highly significant negative correlation between such characters in both species. It is of interest to note that, at lower temperatures, LB populations are superior to UG populations where the former show a higher percentage of emergence and lower variation for wing length, but at the higher temperature the situation is reversed.

Optimal conditions and geographical distribution. There is extensive evidence on *Drosophila* species other than *Drosophila melanogaster* and *Drosophila simulans* which indicates that wing length shows an increase in northern geographical regions, e.g., Stalker and Carsons (1947, 1948 and 1949) on *Drosophila robusta*, Dobzhansky (1948) on *Drosophila pseudoobscura* and Prevosti (1955) on *Drosophila subobscura*.

Our results, summarized in figures 2, 4, and 5, suggest that the optimal temperatures for *D. melanogaster* and *D. simulans* are 25° C and 22° C, respectively. The values of the various characters studied at these optimal temperatures are shown in table 2, the localities being arranged in north to south order.

The results thus presented in table 2 indicate that northern populations, i.e., LB, are significantly larger in size, less variable and more viable than those from the extreme south, i.e., UG populations. In *D. simulans* there is a gradient of size from north to south, while in *D. melanogaster* flies from central Egypt are the smallest. Such differences in behavior and the insignificant differences between some of the Egyptian populations and that from Uganda could be explained on the basis of possible immigration throughout the Nile Valley. LB populations are isolated from the Egyptian ones by the Sinai Desert. If we consider LB populations as northern populations and all other populations, i.e., from Egypt and Uganda, as southern ones, we find significant differences between them in every respect; the former populations are larger, less variable and more viable than the latter ones, which agrees well with the findings of other investigators.

It seems probable, therefore, from such results, that the geographical differences in morphology are the results of an adaptation to climate and such adaptation may be of indirect effect. Dobzhansky (1937) stated that the morphological phenotype may be the by-product of some more fundamental physiological adaptation. Annual mean temperature as well as percentage humidity are the more obvious environmental conditions, which show correlations with the

TABLE 2. *Morphological differences between males and females of* Drosophila melanogaster *and* Drosophila simulans *in mean wing and thorax length, at their optimal temperatures, with their respective coefficients of variation (C.V.%). Units of measurement are 1/100 mm. Percentages of emergence are also presented.*

Population	Wing Length*				Thorax Length*				Percentage of emergence
	Males		Females		Males		Females		
	Size	C.V.	Size	C.V.	Size	C.V.	Size	C.V.	
Drosophila melanogaster									
LB	183.41	1.86	211.09	1.70	93.69	2.40	106.11	2.19	76.18
UF	175.59	1.97	203.19	2.11	89.48	2.59	102.39	2.19	68.70
WD	176.10	2.29	202.60	1.97	91.40	3.37	104.74	2.45	63.13
LX	176.16	2.36	203.78	1.99	90.81	2.64	103.87	2.22	73.89
UG	180.03	2.50	210.27	2.36	91.54	3.41	105.03	2.57	58.11
Drosophila simulans									
LB	190.91	2.17	220.16	1.87	95.63	2.96	109.95	2.36	79.91
UF	189.36	2.77	218.66	2.19	94.75	2.84	108.39	2.27	72.59
WD	184.97	2.73	209.63	2.49	91.20	3.52	104.54	3.03	74.84
BS	189.44	2.25	217.98	1.79	94.81	2.86	108.86	2.66	74.83
UG	185.96	2.58	215.52	1.99	92.41	3.21	107.31	2.47	69.49

* Each mean is taken from 200 pairs of adult flies.

phenotypic appearance of the animal. Other environmental conditions such as type of flora may have some effects on such adaptation. In sum, we find that animals which are adapted to a given temperature are less phenotypically variable than those not adapted.

Sex-ratio. It is a known fact that wild populations of *Drosophila* give a sex-ratio almost of 1:1 under optimal conditions. When environmental conditions are changed the ratio is also changed.

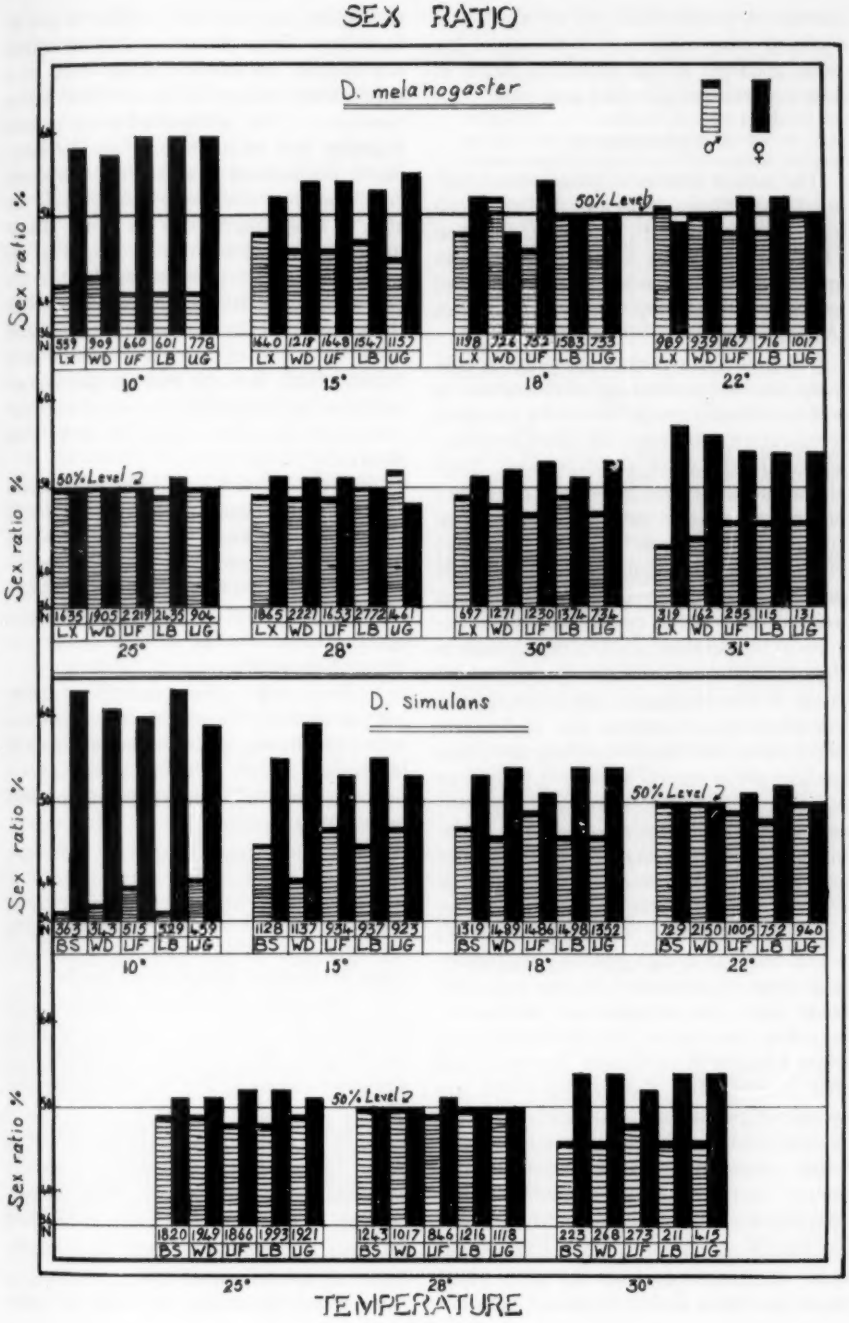
There are some exceptional situations reported in which some wild-type females captured from nature give rise to a highly abnormal sex-ratio. Thus, Magni (1954), Moriwaki et al. (1957) working on *Drosophila bifasciata*, Cavalcanti and Falcau (1954) on *D. prosultans*, Stalker (1957) on *D. paramelanica* and Malogolowkin et al. (1959) on *D. willistoni*, all reported abnormal sex-ratio arising from some wild females. Malogolowkin et al. (1959) attributed such an abnormal situation to the action of an agent which is transmitted by the female to all her eggs and is lethal in XY zygote.

In the present investigation, all hatched flies were classified to sex and the results for the various sex-ratios at the different temperatures are presented in figure 6 a and b for *Drosophila melanogaster* and *D. simulans*, where locality and total number of adults counted are also shown.

The results as shown in figure 6 indicate an influence of temperature on sex-ratio. At lower and higher temperatures in both species there are significant differences between sexes; females predominate, while at milder temperatures the ratio is almost one to one. During the experiment it was noticed that at the two extremes of temperature, particularly at the higher one, pupae fail to develop into adults. It was observed that adults attempted to emerge from the pupae, but only succeeded in dragging their heads and thorax out of the pupal case.

One may conclude from these results, that females are the stronger sex in resisting

FIG. 6. Sex-ratio for all populations of *Drosophila* under various degrees of temperature; populations and number of adults counted in each locality are also illustrated.


SEX RATIO
D. melanogaster
♂
♀
Sex ratio %
50% Level
559 909 660 601 778
LX WD UF LB UG
10°
1660 1218 1648 1547 1157
15°
1198 726 753 1583 733
18°
989 939 1167 716 1017
22°
50% Level 2
1635 1905 2219 2435 904
25°
1865 2221 1653 2772 1441
28°
697 1271 1230 1374 734
30°
319 142 255 115 131
31°
D. simulans
363 343 515 529 459
BS WD UF LB UG
1128 1137 934 937 923
1319 1489 1486 1498 1352
729 2150 1005 752 940
1820 1949 1866 1993 1921
1243 1017 846 1216 1118
225 268 273 211 415
TEMPERATURE

changes in temperatures and are also better buffered than males. Such resistance became apparent in the immature stages of adults, particularly in the pupal stage.

Conclusions

The earliest studies of geographical variation in different species of *Drosophila* have been reviewed by Stalker and Carson (1947). It has been found that size of an animal differs according to altitude and northern animals are larger in size than southern ones.

Our results as reported, show clearly that body size and percentage of emergence as well as sex-ratio can be altered by changing temperature conditions; the latter two characters are the more sensitive ones. Such alteration in the new laboratory conditions depends to a great extent on the original climatic conditions in which flies had survived. Thus, LB populations of *Drosophila melanogaster* and *Drosophila simulans* are well adapted to the colder and milder degrees of temperature and UG populations to the warmer ones. Such populations are larger in wing length and thorax length with low phenotypic variances and higher viability under their adapted conditions. These findings are in general agreement with those of Lerner (1954) who stated that the poorest adapted individuals have higher variability. Since variability is usually regarded as a measure of homeostasis, on the assumption that a less variable phenotype indicates superior homeostatic buffering properties which result in a high general adaptedness in a range of environments, one may conclude that LB populations which are euryokous populations are more adapted to wider changes in environmental conditions than that of UG populations which are stenokous populations. An analysis of the geographical distribution of the two populations, shows that LB populations inhabit regions characterized by medium summer temperature and colder winter with a lower percentage of humidity, while UG populations were captured from a region where the temperature is 27° C almost constant throughout the year with a higher degree of humidity. Thus indicating that stenokous populations are better adapted only to a temperature similar to that of their native conditions. This is expected since natural selection acts more strongly on the euryokous populations than on the stenokous ones, therefore the former populations are able to adapt themselves to wider alterations of climatic conditions, i.e., they are more homeostatic. Results obtained in the present investigation are in agreement with those reported by Lewontin (1956 and 1957) who has equated homeostasis with fitness, which indicate that the physiological and morphological responses of a homeostatic individual are adaptive so as to favor survival.

The reaction of LB and UG populations to the temperatures, showing different adaptation to the extremes, gives rise to the following questions:

1. What would be the response to selection in populations of both localities under optimal conditions as well as colder and warmer temperatures?

2. Do crosses between and within different populations, under the previously mentioned conditions, yield the same degree of heterosis?

Such points will be investigated in future experiments.

Summary

1. Natural populations of *Drosophila melanogaster* and *Drosophila simulans* were captured from different geographical regions in Lebanon, Egypt, and Uganda.

2. Offspring of such populations were reared under different temperatures ranging from 10° to 31.5° C in *Drosophila melanogaster* and to 30.5° C in *Drosophila simulans*.

3. Wing and thorax length are greater at lower temperatures, decreasing gradually with increasing temperature, while the percentage of emergence is lower at the two extremes of temperature and significantly higher at optimal conditions.

4. Wing/thorax ratio is about 2 under

optimal conditions, increasing at lower temperatures and decreasing at higher ones.

5. Phenotypic variance of wing length is higher at both extremes, and much higher at warmer temperatures.

6. Complete sterility, i.e., eggs failing to produce adults, occurs at 31.5° C in all populations of *Drosophila melanogaster* and at 30.5° C in *Drosophila simulans*.

7. Lebanon populations, i.e., northern populations, are more vigorous, less variable and more viable than all other populations studied at almost every temperature, while populations from Uganda show superiority to all other populations only at the higher temperatures, i.e., their original climatic conditions.

8. Extremes of temperature adversely affect sex-ratio. At the two extremes of temperature females appear to be the stronger sex and are significantly more numerous than males. At milder temperature the sexes occur in equal numbers.

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MIMETIC ASSEMBLAGES OF SIBLING SPECIES OF LYCID BEETLES

E. G. Linsley, T. Eisner, and A. B. Klots[1]

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Lycid beetles, throughout the tropical and subtropical regions of the world, serve as models for a great many Batesian mimics and participate in numerous Müllerian mimicry complexes. Their broad elytra, aposematic coloration, gregarious habits and sluggish behavior admirably suit them for this role. These characteristics are universal and unrelated species from various continents are often superficially identical in coloration and behavior. The family probably represents the most ancient living group of models for mimetic insects. Carpenter (in Carpenter and Ford, 1933) summarizes lycid mimicry as follows:

"They are resembled in colour and pattern by members of every order of Insects whose bodily form yields the foundation on which a Lycoid appearance can be built. Among *Lepidoptera* the Lycoid moths belong to families of sedentary habit which keep the wings flat over the back or even folded round the body. The *Hymenoptera* have not the shape of body which could produce a Lycoid appearance, but the necessary aposeme is shown by the wings, which in different families are orange with black tips and when lying over the back reproduce the Lycoid effect: there are Lycoid wasps of several families, Saw-flies, and Ichneumon-flies. Two-winged flies (*Diptera*) are known from several families, among which may be mentioned *Asilidae*.

"The sucking bugs (*Hemiptera*), in shape essentially similar to beetles, furnish abundant mimics from several families.

"Among the enormous assemblage of beetles themselves there are many families which have produced Lycoid species, and they all are sedentary in their habits: the writer cannot recall any really active beetle mimetic of the *Lycidae*. In some cases the modification has been considerable, so that a Lycoid Longicorn may require close examination to detect the characteristic antennae, modified in length to approximate to the shorter antennae of the model, although the numerous joints are there. The typical parallel-sided elytra are also modified by being widened posteriorly to be more like the expanded organs of the model.

"In all these mimics, which throughout the world must run into many hundreds of species, there is vast difference in the habits and food of the larvae, yet these agree in the one character of producing an adult with Lycoid colouring. They may be vegetarians or carnivores: among the former some feed on dead wood, taking years to mature and living in relatively constant temperature and humidity. Others live freely exposed and feed on leaves, etc., in the open. The carnivorous larvae may hunt their prey themselves in the open, or in dead wood, or may live underground, maturing in a few weeks, and have paralysed living insects supplied them to eat. Others live within the body of their host whose juices they absorb.

"The quality of the food, the manner in which it is obtained, and the environment in which the larvae live are so different that the superficial resemblance of the adults cannot be ascribed to these factors."

Our knowledge of such mimetic assem-

[1] University of California, Berkeley, Cornell University, Ithaca, N. Y., and the City College of New York, respectively. The writers are indebted to Dr. Mont Cazier, Director, Southwestern Research Station, American Museum of Natural History, Portal, Arizona, for making the facilities of the station available for these and related studies. Dr. Cazier, Miss Marjorie Statham, and Mrs. E. G. Linsley ably assisted in the taking of field samples and Mr. George M. Happ and Miss Frances A. McKittrick in tests with predators. Dr. W. L. Brown, Jr., kindly identified the ants, Dr. W. J. Gertsch the arachnids, Mr. J. W. Green the lycid beetles, Dr. Frederick Rindge the geometrid moth, and Dr. Jack McCormick the plants. The study was aided in part by a grant from the Bache Fund of the National Academy of Sciences, and by Grant E-2908 of the U. S. Public Health Service.

blages as those described above, has been largely derived from the tropical regions of the Southern Hemisphere (cf. Marshall and Poulton, 1902; Shelford, 1901, 1917; Gahan, 1913; Carpenter, 1921; Arrow, 1928; Bates, 1892; etc.), and few quantitative data have been published relative to the numerical relationship between models and mimics.

In North America, the most conspicuous lycid beetles belong to the genus *Lycus*. Twelve species are known from within the boundaries of the United States (Green, 1949). Ten of these have been reported to occur in Arizona as follows: *Lycus* (*Neolycus*) *fernandezi* Dugés, *L.* (*N.*) *arizonensis* Green, *L.* (*N.*) *lecontei* Green, *L.* (*Lycostomus*) *sanguineus* (Gorham), *L.* (*L.*) *sanguinipennis* Say, *L.* (*L.*) *fulvellus* LeConte, *L.* (*L.*) *rubescens* (Schaeffer), *L.* (*L.*) *minutus* Green, *L.* (*L.*) *simulans* (Schaeffer), *L.* (*L.*) *loripes* (Chevrolat). Eight species have been recorded from the Huachuca Mts. (Schaeffer, 1908, 1911; Green, 1949) and at least six have now been found in the Chiricahua Mts.

During the last two weeks of July, 1959, the authors were privileged to study the composition of a mimetic assemblage associated with *Lycus fernandezi* Dugés and its sibling *L. arizonensis* Green and a parallel assemblage centered about *L. loripes* (Chevrolat) and its sibling *L. simulans* (Schaeffer). Both assemblages were found together on the grounds of the Southwestern Research Station of the American Museum of Natural History.

The Locality

The Southwestern Research Station is located about 5 miles west of Portal, Arizona, above Cave Creek Canyon, Chiricahua Mountains, at an elevation of 5,400 feet. The area surrounding the station has been subjected to a great deal of ecologic disturbance and contains many plants not indigenous to the region. It is mostly comparatively xeric, but the strip adjacent to a small stream along one edge of the station grounds, which flows only during the rainy season, is markedly hydric. The area is, therefore, somewhat of an ecotone between xeric upland and the hydric canyon bottom. The former is characterized by Chihuahuan pine (*Pinus chihuahuana* Engelm.), alligator-barked juniper (*Juniperus deppeana* Staud.), Emory Oak (*Quercus emoryi* Torrey) and Arizona white oak (*Quercus arizonica* Sarge.). The latter is characterized by sycamore (*Platanus wrightii* Wats.), at least three willows (*Salix* spp.), cottonwood (*Populus fremontii* Wats.), box elder [*Acer negundo* var. *interius* (Britt.) Sarg.] and Arizona walnut [*Juglans major* (Torr.) Heller].

On the grounds of the Station, the principal laboratory building faces northward. Directly opposite the main entrance, across an access road and parking area, is a triangular-shaped meadow bounded on the south by about 160 feet of the access road, to the west by pathways, and to the northeast by a row of trees. In mid-July this meadow was dominated by masses of white sweet clover (*Melilotus alba*) at the peak of bloom. Some of the plants were six and one-half feet tall, or more, but most averaged about four and one-half feet. Four major congregating sites for lycids occurred in the meadow. The largest (Site A) was the more easterly and involved an area of about 1,800 square feet. The remaining sites (B, C, and D) occupied about 200, 150, and 400 square feet respectively. The last site was an experimental area enclosed by a fence to prevent plant injury by browsing deer. In each site aggregations of *L. fernandezi* and *L. loripes* occurred together on the same plants, along with their siblings and mimetic assemblages. However, the former was most numerous in site A, the latter in sites B, C, and D.

Sampling and Estimating the Composition of Aggregations

In order to obtain some indication of the relative abundance of models and mimics in the two assemblages without seriously affecting the populations, it was necessary to take samples with a minimum of disturb-

TABLE 1. *Proportionate representation of various elements in samples of mimetic assemblages associated with* Lycus fernandezi *Dugés and* L. loripes (*Chevrolat*)

L. fernandezi complex	Date of Sample			
	July 16		July 24–26	
Lycus fernandezi	43 ♂ ♂	19 ♀ ♀	48 ♂ ♂	24 ♀ ♀
Lycus arizonensis	5 ♂ ♂	2 ♀ ♀	13 ♂ ♂	4 ♀ ♀
Elytroleptus apicalis	3 ♂ ♂		1 ♂	1 ♀
Seryda constans	—	—		1 ♀
Ptychoglene coccinea		2 ♀ ♀		1 ♀
L. loripes complex				
Lycus loripes	64 ♂ ♂	55 ♀ ♀	232 ♂ ♂	83 ♀ ♀
Lycus simulans	1 ♂	2 ♀ ♀	4 ♂ ♂	4 ♀ ♀
Elytroleptus ignitus	2 ♂ ♂		1 ♂	1 ♀
Eubaphe unicolor	2 ♂ ♂	1 ♀	—	—

ance. On July 16, the field population of the *Lycus fernandezi* type was estimated by visual examination at about 250 individuals. By random sweeping, members of this complex were captured until it was estimated that about 75 had been taken (for the actual count, see below). The population of the *loripes* complex was larger, by visual estimate about 2,000, and an attempt was made to capture a sweep sample of about 150 individuals. During the next 10 days visual examinations of the assemblages were made, plant by plant, and the presence of mimics noted. On July 24 and 25, all of the mimics which could be found were removed from the aggregations for use in feeding experiments with predators. On July 26, all of the remaining lycids were collected. This procedure provided data on the relative abundance of the lycid siblings and on the relative numbers of the sexes. (table 1).

THE *LYCUS FERNANDEZI* MIMETIC COMPLEX

Lycus fernandezi Dugés (figs. 1, 2) was originally described from Guanajuato, Mex-

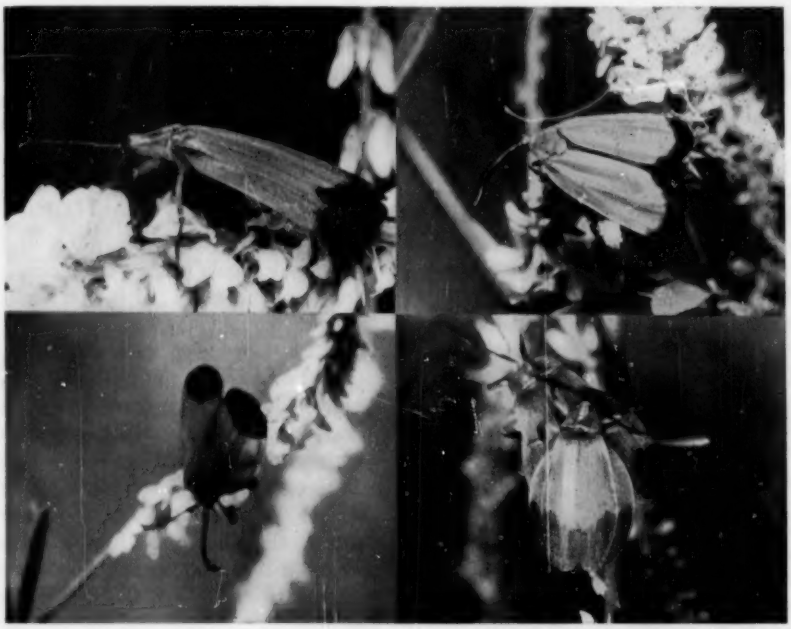

FIG. 1. Members of the *Lycus fernandezi* mimetic complex photographed *in situ* while feeding at florets of *Melilotus alba*. Upper left, *L. fernandezi* Dugés; upper right, the moth *Seryda constans* (Henry Edwards); lower left, *Lycus arizonensis* Green; lower right, mating pair of *L. fernandezi*, with second male beneath right elytron of female, presumably feeding on secretions at base of abdomen.

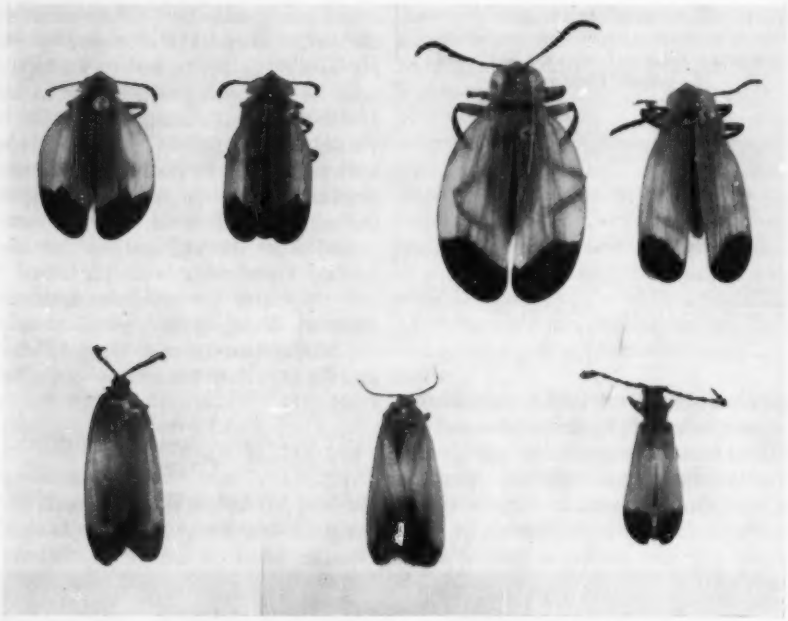

FIG. 2. The *Lycus fernandezi* mimetic complex. Upper left, *L. fernandezi* Dugés (male left, female right); upper right, *L. arizonensis* Green (male left, female right); lower left, *Seryda constans* (Henry Edwards), lower center, *Ptychoglene coccinea* (Henry Edwards), lower right, *Elytroleptus apicalis* LeConte.

ico. It is a widespread species in northern Mexico, extending into southwestern United States at least as far as central Texas, southern New Mexico and central Arizona. As a model for mimicry it has the following superficial characteristics: (1) it is a large species, ranging in length from 10 to 18 mm, with the elytra very broadly dilated in the male, less so in the female, (2) the color is a conspicuous orange-yellow, with the apical one-fourth of the elytra, and the antennae, tibiae, and tarsi black (the apical black spot varies somewhat in different geographical regions, but in the Chiricahua Mountains the anterior margin is almost always distinctly notched on the humeral costa), (3) it gathers gregariously on flowering shrubs for feeding and mating, (4) it feeds on nectar, and thus is available as a model for a variety of potential mimics among other nectar (and pollen) feeding insects in both its aggregating and dispersed phases, (5) it is slow-moving as it crawls over the flowers, (6) the mating pairs remain together for long periods of time (the broader male usually completely covering the female), (7) it is slow and conspicuous in flight, the hind wings also being black-tipped, (8) it bleeds freely, the slightest injury bringing forth a large drop of blood, and (9) it appears to be avoided in varying degrees by a variety of vertebrate and invertebrate predators.

Lycus arizonensis Green (figs. 1, 2), presumed to be a species sibling of *L. fernandezi*, is slightly larger in average size (range 12–18.5 mm) but is almost identical in form and coloration. The only superficial difference between the two is the absence of a notch in the anterior margin of the elytral spot at the point where the humeral costa enters. In comparison with its sibling, it was present in much smaller

numbers during the period in which we made our observations.

Elytroleptus apicalis LeConte (fig. 2), a longicorn beetle of the family Cerambycidae, is a little smaller in average size than *L. fernandezi* (our sample ranged from 10–13 mm in length), and the elytra are less broadly dilated. However, in coloration the two are practically identical, even to the notch in the anterior margin of the apical black spot on the elytra. The longicorns were seen crawling over the blossoms in the lycid aggregations, but were not abundant (see table). They are thought to be nectar and pollen feeders, although *Melilotus*, a rich nectar source, is generally regarded as a poor pollen plant.

Seryda constans (Henry Edwards) (fig. 2), a moth of the family Pyromorphidae, is a diurnal species which visits flowers, and apparently mimics *L. fernandezi* under dispersed as well as in congregated situations. When sipping nectar and crawling over the blossoms, it keeps the wings folded flat over the back, beetle-like. It approximates the lycid in size, our examples ranging from 12–15 mm in length with the wings folded. The ground color is very similar to that of the model. The appendages are also black, as are the distal margins of the forewings, although these last are usually narrower. Individuals, although rare in the aggregations (they were captured twice, observed three times), were found in small numbers in the general area and occasionally came to light.

Ptychoglene coccinea (Henry Edwards) (fig. 2) and *P. phrada* Druce, moths of the family Lithosiidae, are also diurnal flower visitors. Their ground color is bright red rather than orange-yellow; but, since we know little or nothing about the qualitative color vision of the predators involved, it may well be that this difference is of little or no significance. As in *Lycus fernandezi* the appendages and the distal margins of their forewings are black, but the black wing areas are usually more extensive than those of the beetles. The head and thorax of *P. coccinea* are red, of *P. phrada*, black. There appear to be constant, although slight, genitalic differences between them in both sexes. Both species range widely in Arizona, and both have been taken previously in some numbers at the Southwestern Research Station from late June to mid-August. Like the lycids described above, they constitute a pair of sibling species. However, we have no evidence as to whether or not there is a connection between the evolution of the sibling pairs of beetles and this sibling pair of mimetic moths. In 1959 *P. coccinea* was found several times crawling over the blossoms in the lycid aggregations, as well as in scattered situations; and its presence in the company of the beetles appears to be of mimetic significance. The subsequent discovery of still another Müllerian assemblage, which might well provide models for these moths suggests that in other areas they may be mimetically associated with a more appropriately colored group of lycids. These include *Lycus* (*Neolycus*) *lecontei* Green (fig. 4), the Arizona form of which is rufous or scarlet with the head, antennae, palpi, tibiae, tarsi and apical one-third of the elytra black. Although this species has not yet been reported from the Chiricahua Mountains, the superficially similar *Lycus* (*Lycostomus*) *sanguineus* (Gorham) (fig. 4) has been found there along with the gregarious, vinegar-smelling cantharid *Chauliognathus profundus* LeConte (fig. 4). This last, although narrower in form than the *Lycus*, is similar in size and coloration and gathers by the thousands on flowering shrubs such as *Baccharis*. However, in the vicinity of the Research Station, it did not appear in numbers until the first week of September, long after the lycid aggregations had dispersed. Whether these moths owe their coloration to the presence of any or all of these red and black beetles remains to be determined.

A number of other diurnal, flower visiting moths, presumably mimetic, are associated with lycids elsewhere in the Southwest and northern Mexico. These are discussed below.

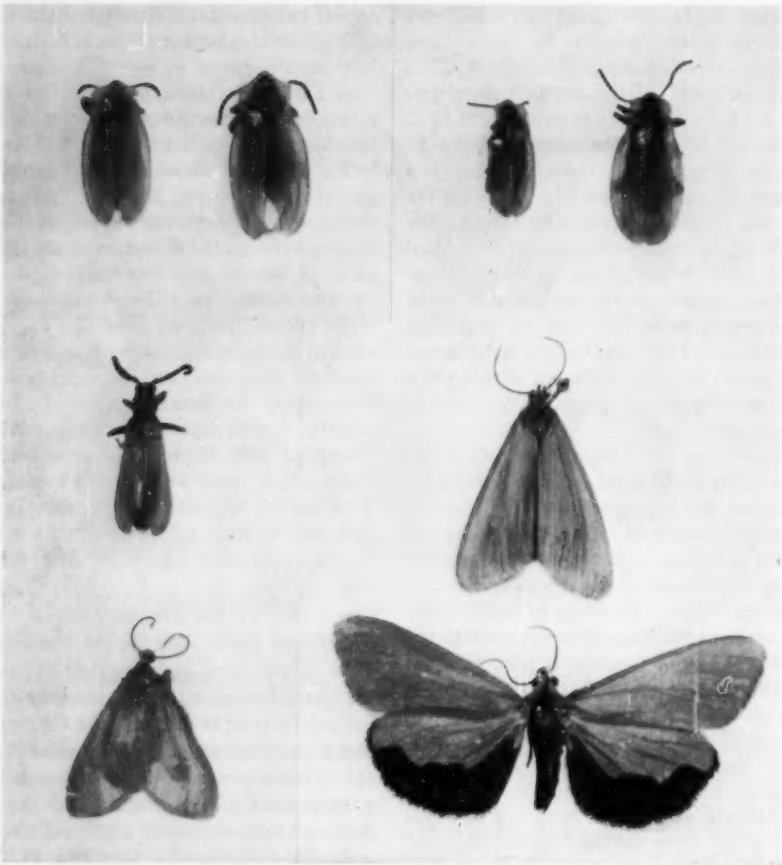

FIG. 3. The *Lycus loripes* mimetic complex. Upper left, *L. loripes* (Chevrolat) (male left, female right); upper right, *L. simulans* (Schaeffer), (female left, male right); center left, *Elytroleptus ignitus* LeConte; lower left, *Eubaphe unicolor* (Robinson); center right, *Holomelina ostentata* (Henry Edwards) with wings folded; lower right, same with wings spread to show aposematic hind pair.

THE *LYCUS LORIPES* MIMETIC COMPLEX

Lycus loripes (Chevrolat) (fig. 3) was described originally from Mexico. It is a widespread, common species, and is known from many localities in southern Arizona (especially in the Chiricahua, Huachuca, Santa Rita, Santa Catalina, Coyote, Dragoon, and Baboquivari mountains). The species is smaller on the average than *L. fernandezi*, ranging in length from 10–13 mm, and is concolorous yellow-orange with some black on the appendages. The elytra of the male are scarcely dilated. The beak is long and slender, being equal to about twice the distance between the eyes. Although less conspicuously marked than *L. fernandezi*, it was more numerous in our study sites and the individual aggregations were larger. Like *L. fernandezi*, these beetles are assumed to be nectar and pollen feeders, and apparently share with that spe-

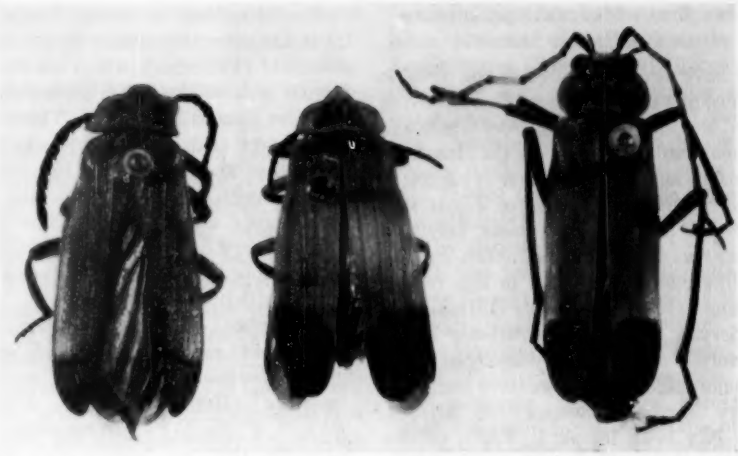

FIG. 4. *Lycus sanguineus* (Gorham) (left), *L. lecontei* Green (center) and *Chauliognathus profundus* LeConte.

cies most of the characteristics which make it a suitable model for mimetic forms.

L. simulans (Schaeffer) (fig. 3) is a superficially identical sibling species of the same size and coloration as *L. loripes*. It differs by having a short beak, which is less than one and one-half times the distance between the eyes, and in proportions of the antennae and the shape of the palpi. In our observation plots it was represented in small numbers, like the sibling of *L. fernandezi*.

Elytroleptus ignitus LeConte (fig. 3), a longicorn beetle, is a little smaller in average size than *Elytroleptus apicalis* (our sample ranging in length from 8–11 mm), and the elytra are concolorous yellow-orange. However, it is the counterpart of *E. apicalis* in the *L. loripes* mimetic assemblage. It has similar habits and in our site the two species were present in about equal number.

Eubaphe unicolor (Robinson) (fig. 3), a yellow-orange geometrid moth, appears to be a lycid mimic in the *loripes* aggregations and under dispersed conditions. The wings are concolorous, the antennae black, and when at rest or crawling over the blossoms with wings folded it varies in length from about 10–14 mm. The moths were found seven times among the lycid aggregations, usually in the early morning or when the sky was overcast. Individuals also came to light in small numbers during the period when the lycids were congregating.

Holomelina ostenta (Henry Edwards) (fig. 3), a moth of the family Arctiidae, is slightly larger than the preceding (and considerably larger than the lycids) and differs by having bright red and black hindwings. However, when at rest the forewings, which are concolorous yellow-orange with darker fringes, are folded back flat, providing lycid coloration. This species was not found in the lycid aggregations and its abundance about the lights suggests that it may be primarily a nocturnal species. Possibly it benefits generally from the presence of the lycids in the area when it is at rest during the day. Various other species of *Holomelina* are widely distributed in North America; and many occur in regions lacking possible lycid models. Some have the forewings dark brown, others, as in *ostenta*, bright yellow-orange or orange-brown. Essentially nocturnal, many are active during the daytime, especially in grasslands and open habitats where they fly up in numbers when disturbed, and are then very conspicuous, and they sometimes visit flowers.

Other *Lycus* Mimetic Assemblages in the United States

We have already alluded to the possible existence of a mimetic assemblage involving the red and black *Lycus lecontei* Green and *L. sanguineus* (Gorham). In the Huachuca Mountains another assemblage is suggested by the occurrence together of *Lycus sanguinipennis* Say and the mimetic longicorn *Elytroleptus rufipennis* (LeConte). Several lycid-like moths also occur in this region, including *Ptychoglene phrada* (Lithosiidae) and *Seryda constans*, *Tetraclonia dyari*, *Pyromorpha rata*, and *Pyromorpha fusca* (Pyromorphidae) which we have seen from Ramsey Canyon, Huachuca Mts., Arizona, 10–15 July 1941, leg. A. B. Klots, visiting *Melilotis alba* and Compositae, although no record was kept of the lycids associated with these moths. The first two species have already been discussed. *Tetraclonia dyari* and *Pyromorpha rata* have the forewings yellow-brown to orange-brown, with dark distal margins, and may fit into the *Lycus fernandezi* complex. *Pyromorpha fusca*, which has the wings solidly fuscous but the head, thorax and abdomen dull yellow, may mimic almost any of the small, dark lycids.

In eastern North America only one species of *Lycus* occurs, *L.* (*Lyconotus*) *lateralis* Melsheimer. It ranges from Maine south to Florida and west to Illinois, Missouri, Kansas, and Texas (Green, 1949). *L. lateralis* differs markedly in coloration from the red, orange or yellow and black patterns characteristic of the majority of the southwestern members of the genus, being black, with the elytral humeri and the sides and apex of the pronotum fulvous. However, it closely resembles lycids of other genera that occur in the same area. It has its complement of mimics, including the longicorns *Elytroleptus floridanus* (LeConte) and *Euryptera lateralis* (Olivier), which also differ from their brightly colored southwestern[2] congeners.

Also widespread in eastern North America is the extremely similar lycid *Caeniella dimidiata* (Fabricius), which has the basal fulvous area of the elytra somewhat more extensive than in *L. lateralis*. There can be little doubt that these lycids supplement each other aposematically. However, the most common eastern lycid is the somewhat larger *Calopteron reticulatum* (Fabricius), of very different but strikingly aposematic appearance, the elytra being crossbanded with black and orange.

A number of diurnal, flower-visiting pyromorphid moths occur with *L. lateralis* and *C. dimidiata*. Of these, *Pyromorpha dimidiata* (Herrich-Schäffer), (Holland, 1917, Pl. 47, fig. 33) which has smoky black forewings that are basally dull fulvous, matches *L. lateralis* very closely, *C. dimidiata* less well. *Acoloithus falsarious* Clemens, a smoky black moth with orange collars, has considerable resemblance to *L. lateralis*. Also, the ctenuchid moth *Lycomorpha pholus* (Drury) is an extremely good mimic of *C. dimidiata*, having about the same relative amount of bright orange basally on the forewings, the two apparently constituting an intimate Müllerian mimetic pair. Finally, a number of other pyromorphid moths in eastern and western North America, belonging to the genera *Pyromorpha* Herrich-Schäffer, *Triprocris* Grote, *Acoloithus* Clemens, and *Harrisina* Packard, are small, smoky-black winged, diurnal flower visitors that must be involved to a

[2] For example, *Euryptera ignita* Schaeffer and *E. cruenta* Martin, both from the Huachuca Mountains, are red or reddish-orange with black appendages. These species have retained their somewhat slender, lepturine ancestral form; but in tropical America a number of species have not only lycid-like markings but also flattened, expanded antennae and flared, costate elytra. Some of these, such as *E. latipennis* Serville and *E. lyciformis* Pascoe, occur sympatrically with more slender but identically marked species which appear to have the same lycid models. In some Brazilian localities, both *E. melanura* Redtenbacker and *E. dimidiata* Redtenbacker have counterparts with expanded elytra. In Mexico, *E. longipennis* Bates is slender; *E. patricia* Bates is broadened. Like many lycid mimics the species of *Euryptera* are mostly rare in collections and in great need of taxonomic study. Belon (1897) has provided a superficial color key for the separation of many of the described species, but it is incomplete and not definitive.

greater or lesser extent in the dark-winged lycid mimicry complexes.

Relative Edibility of Lycids by Predators

A considerable amount of evidence has accumulated indicating that lycids are avoided by vertebrate predators, including lizards, birds, and monkeys. Marshall and Poulton (1902) offered six species of *Lycus* from Mashonaland to baboons and a kestrel and these were rejected, along with several other similarly marked beetles which made up a portion of an extensive Müllerian mimicry complex. Carpenter (1921) also offered African lycids to two young *Cercopithecus* monkeys. His experiments were conducted either by collecting insects at random from their natural surroundings and putting them down so that the monkey could study them, or by taking the monkey into open bush country on a long lead and making exact notes on what it did or did not do. Seven species of lycids were involved (of the genera *Lycus*, *Chlamydolycus*, and *Merolycus*). They all had a single scheme of coloration: orange or orange-brown with appendages black or black and orange and the tips of the elytra black. They lived freely exposed and large numbers were to be found congregated on a single flowering shrub. One of the monkeys put all lycids tested in the most distasteful class. Only twice in ten trials were they tasted, even under the influence of hunger, and no part was eaten (*Merolycus femoralis* Bourg. was tasted once and refused on the second occasion when the subject was less hungry). When an example of *Lycus constrictus* Fahr. was offered with the elytra pulled off, it gave off a strong odor and the subject would not accept it. Only two lycids were offered to the other monkey. One of them was eaten (*Chlamydolycus trabeatus* Guér.), but the other was tasted and then rejected.

In the West Indies, Darlington (1938) studied the mimetic assemblage associated with two blue-tipped yellow lycid beetles, *Thonalmus suavis* Jacquelin Duval, and *T. aulicus* Jacquelin Duval. These lycids were treated as inedible by the principal vertebrate predator of the region, the lizard *Anolis sagrei* (Duméril and Bibron). Not only were the lycids consistently refused, but so also were four species of *Thonalmus*-like Cerambycidae (although six other plainly marked species were eaten). Parsons (1940) tested one of the *Thonalmus*-like species (*Trichrous pilipennis* Chevrolat) by placing it in the mouth of an *Anolis* which had just rejected a *Thonalmus*. It was swallowed at once, suggesting that it is edible, although ignored in nature.

At Martha's Vineyard, Massachusetts, Jones (1932), in nine experiments offered 47 *Calopteron reticulatum* Fabricius to seven species of birds on feeding trays together with 519 other kinds of insects. After 141 visits by birds, 41 of 47 *Calopteron* remained, although 155 of 157 other beetles were eaten. Four of the six *Calopteron* were taken in one experiment when the only bird visitors were blue jays (*Cyanocitta cristata* Linnaeus). Jones also points out that this species does not appear among the 337,000 insects identified with the stomachs of 80,000 birds tabulated by McAtee (1932). Jones did not utilize moth mimics of *Calopteron* in his experiments, but his lists include two species of *Lycus* mimics, *Pyromorpha* (as *Malthaca*) *dimidiata* Herrich-Schäffer (Pyromorphidae) and *Lycomorpha pholus* Drury (Ctenuchidae). Although the presumed model for these moths, *Lycus lateralis* Melsheimer, was not offered on the feeding trays, the single example of *Lycomorpha pholus* offered was left on the tray, as were four of five *Pyromorpha dimidiata* offered in three experiments.

Virtually nothing seems to be known about how repellent lycids are to invertebrate predators. The single observation known to us is that by Darlington (1938), who saw "an Asilid fly catch a small black and red Lycid in the air, but immediately released it."

Our own experiments with predator-prey encounters took place within special observation cages, the confines of which were

made to resemble when possible the natural surroundings of the particular predator being tested. None of the predators were starved for excessive periods of time prior to the experiments. In cases where a *Lycus* or one of its mimics was ignored or rejected, additional prey (usually dealate moths or scarab beetles) was offered immediately thereafter in order to determine whether the predator was actually discriminating or merely reluctant to take food.

Of the predators tested by us, it is likely that only the mantids, wasps, jays, and the lizard *Sceloporus jarrovi* are of significance as enemies of the particular lycid associations studied. The other test predators were ground foragers, and some, such as the horned toad, whiptail lizard, turtle, and grasshopper mice, were not found in the immediate vicinity of the station. Our reason for using such predators, whether or not they occurred in the special habitat under investigation, was to try to determine how general or predator-specific the repugnatorial effectiveness of lycids is.

A. Invertebrate Predators

1. *Lycosid spiders* (*Lycosa carolinensis texana* Montgomery). Four female spiders were each offered a single *Lycus* (three of the concolorous *loripes* type, one of the black-tipped *fernandezi* type). During the following fifteen minutes only one (concolorous) was eaten. Although the other three were ignored, it is probable that, being of rather slow and even gait, they simply escaped detection. More vivacious prey offered as a choice thereafter was promptly eaten.

2. *Whip scorpions* [*Mastigoproctus giganteus* (Lucas)]. None of the six whip scorpions made attempts to seize the lycids offered, although all of them captured other insects of comparable size given them shortly thereafter. Perhaps again the *Lycus* simply failed to make themselves apparent. Whip scorpions resemble lycosids in that they respond best to jerkily moving prey.

3. *Solpugids* (*Eremobates* sp.). Three solpugids were each given a single *Lycus* (two concolorous, one black-tipped). They were all seized instantly, but were immediately released. Only one of the lycids showed noticeable injury as a result of the encounter. It received a marginal cut in an elytron from which it recovered fully, showing no noticeable abnormality as late as two days thereafter. It might be argued that the solpugids had not really been repelled, but had merely performed some kind of defensive maneuver. This is unlikely, however. The same solpugids were also offered an abundance of other arthropods, and of these, the only few that were rejected in a manner similar to the lycids possessed in all cases some kind of chemical defense mechanism (*Eleodes*, *Brachynus*, *Mastigoproctus*).

4. *Ant-lion larvae* (unidentified). Three concolorous and one black-tipped *Lycus* were tossed into pits and were instantly seized and eaten. The hollow, sucked-out carcasses were found just outside the pits several hours later. These ant-lions died before pupation, but this may have resulted from improper subsequent treatment.

5. *Preying mantids* (*Stagmomantis limbata* Hahn). In one series of tests, five encounters were witnessed, involving four different mantids striking at three concolorous and two black-tipped *Lycus*. In each case the beetles were released within seconds, and of the two that showed noticeable injury, only one died. Following these experiments, about one dozen *Lycus* were left in confinement with the four mantids for four days, at the end of which time none had been eaten. In another series of tests two half- and two full-grown mantids were offered three mimetic moths [two *Eubaphe unicolor* (Robinson), one *Seryda constans* (Henry Edwards), and one mimetic longicorn (*Elytroleptus apicalis* LeConte)]. All except the *Seryda* moth were devoured readily (this last was only partly eaten). Subsequently two were offered black-tipped *Lycus*, two concolorous. Three rejected the lycids immediately upon contact, one ate a black-tipped specimen and then refused contact with further lycid specimens.

The example that refused the black-tipped lycid after contact, subsequently became very agitated and refused and ran away from all prey subsequently offered, including flies and dull colored moths. After five days this specimen died. On another occasion, a nymph of this mantid was offered some lampyrids in Connecticut. It seized one, bit it, immediately dropped it, rubbed its mouthparts with a foreleg for a minute or two, and rejected regular food (tettigoniids) for half an hour. A second trial the following day produced the same result. No further tests were made, however, and the mantid survived and transformed successfully to the adult.

6. *Ants* [*Pogonomyrmex occidentalis* (Cresson)]. Six concolorous lycids were released one at a time a few inches away from the nest entrance of a natural colony. The ants attacked singly or in groups of two or three, but no ant remained in the vicinity of a beetle for more than a few seconds at a time. During this period they seized appendages and tugged at the wing margins, but as far as could be observed, they never persisted long enough to actually pierce the cuticle. The beetles walked away slowly, continually accosted, but never seriously hampered. Each eventually reached safety.

On the basis of comparable experiments by one of us (Eisner) with this ant and the related *P. badius*, involving a wide variety of insects, a rapid overpowering of the lycids would have been predicted, particularly near the nest entrance where the ants are highly aggressive. Ordinarily, when the ants grasp an insect with the mandibles, they do not relinquish their hold, but persist tenaciously, and as a rule also attempt to sting. They soon accumulate in swarms, and insects more vigorous than lycids (e.g., nymphs of *Periplaneta*) have been seen to be seriously hampered in their escape, and sometimes even completely stalled. Only in two exceptional instances were weak and sluggish insects observed to make an essentially unimpeded escape comparable to that of the lycids, and in both cases this involved species known to be protected by chemical means of defense (meloid and coccinellid beetles).

7. *Wasps* (*Polistes canadensis navajoe* Cresson). In a field observation, a female wasp twice seized and twice dropped a single concolorous lycid, after turning it about in its mandibles. The beetle was later examined for injuries but none were found. [Belt (1874) records a hunting wasp in Nicaragua that regularly preys upon "protected" heliconid butterflies, bites off the appendages, malaxates the body, and stores them for the young.]

B. Vertebrate Predators

1. *Lizards*. A mixed cluster of about 12 concolorous and black-tipped lycids was introduced to a cage housing a horned toad, [*Phrynosoma cornutum* (Harland)], two *Sceloporus jarrovi* Cope and one Whiptail lizard (*Cnemidophorus* sp.). Although the lizards watched the lycids crawling about, none attempted to eat them. Since all these lizards except the *Sceloporus* are ground foragers and were taken in dry habitats where the lycids did not occur, their indifference to the lycids must be attributable to reasons other than past encounters.

2. *Ornate Box turtle* [*Terrapene ornata* (Agassiz)]. About a dozen mixed concolorous and black-tipped lycids were offered and were all eaten in rapid succession. The turtle exhibited no behavioral abnormalities during the meal, and showed no detectable after-effects. This experiment was repeated twice on successive days with similar results.

3. *Jay* [*Cyanocitta stelleri* (Gmelin)]. Six *Lycus* (three of each type) were released one at a time into the cage. In each instance the bird descended from the perch, pecked the beetle to death and then pushed it into a crevice in a corner of the cage. This behavior was noted previously in captive *C. cristata* with both edible insects (*Tenebrio* larvae) and less palatable ones (*Brachynus*), particularly in cases where the bird had been well fed previously. However, *cristata* always returned and ate their hidden scraps at a later time; *stelleri* did not do so with the lycids.

4. *Grasshopper mice* (*Onychomys torridus* Coues). In the laboratory these mice regularly received a single daily meal of from 20 to 40 large-sized insects. These were usually eaten in half an hour. A typical meal consisted of about two dozen half inch long scarabs and three or four large sphinx moths.

(a) Mouse No. 1

On the first day, one concolorous and one black-tipped cerambycid mimic (*Elytroleptus ignitus* LeConte and *E. apicalis* LeConte), together with one black-tipped moth mimic [*Seryda constans* (Hy. Edwards)] were offered about midway during a normal meal of about 30 insects. They were all eaten, except for the moth, which was decapitated and rejected, suggesting that the cerambycids were edible, whereas the moth, a pyromorphid, was not.

(b) Mouse No. 2

(Given only concolorous *Lycus*). When offered *Lycus* for the first time, the mouse had not eaten since the previous meal 24 hours earlier. It promptly ate all 25 lycids given, showing no detectable abnormalities or aftereffects. On the following day, the mouse was given another five concolorous lycids, but only after it had already eaten about two dozen other insects. It repeatedly handled and smelled several of the *Lycus*, but released them all again, unharmed. When five more scarabs were then added, it selected them from among the lycids and ate them. No subsequent approach to the lycids was made.

This sequence of experiments was repeated on each of the next two days with the same results, except that on the second day one of five lycids offered was eaten.

(c) Mouse No. 3

On the first day the mouse was offered about ten concolorous *Lycus* and a concolorous *Elytroleptus* cerambycid mimic, after first having received about a quarter of its daily insect ration (1 sphinx, 7 scarabs). The first one seized was a *Lycus*. It was briefly inspected, but was released shortly, uninjured. After a second and finally a third *Lycus* was similarly inspected and released, the mouse ignored the remainder of the batch, including the *Elytroleptus*, which was not discriminated.

On the following day a concolorous lycid was introduced midway through the usual meal. It was ignored without previous inspection. The next day a concolorous *Elytroleptus* was offered in place of the model lycid. It was promptly seized and eaten.

(d) Mouse No. 4

Essentially the same series of experiments were intended as with mouse No. 3, but in this instance the black-tipped *L. fernandezi* complex was utilized rather than the concolorous *L. loripes* complex (a single black-tipped *Elytroleptus* cerambycid was available). Things did not proceed as far as with No. 3. When a group of seven *Lycus* and the cerambycid were offered midway through a meal, the mouse first proceeded to seize two lycids, rejecting them both. The third insect seized was the cerambycid and it was eaten without delay. The mouse proceeded to inspect and reject another three *Lycus*, before finally ignoring the entire group.

C. The "Free Hemorrhage" of Lycids

Lycids are known to exude fluid readily when handled, and it is generally assumed that this fluid contains the repugnatorial factors. Since the fluid can be emitted from virtually any part of the body, Darlington (1938) concluded that it is blood, rather than some special glandular secretion. In the particular Cuban lycids (*Thonalmus* spp.) studied by him, the fluid was found to be pink and produced "from between the abdominal segments ventrally, from lateral and ventral sutures of the thorax, from between the trochanter and femur and the leg, and, most frequently, from both the inner and outer margins of the elytra." The elytra, in fact, with their swollen, tube-like outer margins seemed especially adapted for bleeding.

Darlington further states that the emission of fluid is not autohemorrhage in a strict sense, since it never seemed to occur unless some membrane had first been ruptured. A surprisingly slight amout of pres-

sure sufficed to bring about this rupture and initiate bleeding. The blood did not squirt out nor ooze, but merely flowed steadily to form large drops. He found the blood to be inoffensive when applied to his skin, lips, and tongue. Its taste and odor were mild, "reminiscent of crushed lettuce." Marshall and Poulton (1902) also make brief mention of the emission of the fluid by South African lycids, the fluid being "very strong-smelling" and white.

Our cursory observations confirm but add little to those of Darlington. Neither lycids of the *loripes* nor the *fernandezi* complexes produced detectable amounts of fluid unless injured, as judged by response to prodding and pinching with fine watchmaker's forceps under a microscope, although, a secretion might have been produced beneath the elytra on either the thorax or abdomen, since these regions were not scrutinized. Single viscous drops, light-grey in color, were collected at the site of injury. Three specimens that were chewed and swallowed by one of us (two of the *loripes* and one of the *fernandezi* type) had no apparent astringency or ill-flavor of any kind. A faint odor, vaguely resembling fresh hay, characterized the living beetles, and persisted for at least several days in pinned specimens.

A special effort was made to check on the survival of injured specimens. None of those with injured wings, with punctured appendages, or with single appendages amputated, showed conspicuous abnormalities as late as 48 hours after injury, except for anticipated difficulties in locomotion. Specimens with small single body punctures survived equally well. The only examples that died had been partly crushed with forceps, or had received lengthy incisions. Several specimens showing conspicuous imperfections of the elytra were collected in the field. Since these varied from a small marginal piece to almost an entire missing elytron, it is possible that the injuries were predator-inflicted.

Of special significance appears to be the finding that in many of the predator-prey encounters the lycids were rejected before fatal injury had been inflicted. In fact, often there was no noticeable injury whatever. Clearly, the repugnatorial principles are either not restricted to the blood alone, or if so restricted, they must pass somehow through the cuticle in effectively repellent concentrations. Also, there is likely to be considerable survival even under conditions where the predators involved are still naive, i.e., insufficiently experienced with lycids and hence aggressive toward them. Interestingly, similar observations have also been made frequently with highly protected butterflies (Danaidae, Ithomiidae, Heliconiidae, Acraeidae). Their bodies have a noticeably rubbery feel when pinched. They cease moving when pinched to an extent that would kill an ordinary butterfly, but recover fully in a few minutes. Collectors of these butterflies soon learn not to rely on pinching and immediately papering specimens of these groups. Under natural conditions involving predator attacks, such individuals are likely to survive as reproductive members of the species, while at the same time "teaching" the predator to shun that and similar mimetic species.

As a final comment on possible functions of lycid exudations, we add that during the summer of 1958, John A. Chemsak observing a species of *Calopteron* at Santo Domingo, 15 miles southeast of Simojovel, Chiapas, Mexico, noted the following:

"*Calopteron* (sp. near *reticulatum* Fabricius) were abundant in the Santo Domingo region and in most nearby areas. Adults of both sexes occurred on the upper surface of the leaves of various trees and shrubs. They were sluggish and quiescent, taking flight only when greatly disturbed. On several occasions two or more individuals were found together in what was at first assumed to be a mating posture. Closer examination revealed that some individuals were feeding on small globules of a light colored fluid secreted from the thorax immediately beneath the wings. The secreting individual elevated the elytra and wings to provide access to the site. Usually one individual

fed at a time but on several occasions two were involved. In the sample taken a female was secreting for the benefit of two males. If this is generally the case the behavior is probably related to sexual activity."

In figure 1, a male of *Lycus fernandezi* may be seen with its head (and mouthparts) under the elytra of the female of a mating pair of the same species.

Discussion and Summary

The feeding experiments reported above are not nearly as extensive nor as conclusive as we would have liked, largely because all categories of mimics were present in small numbers. They are nevertheless consistent with the generally accepted conclusion that lycids are distasteful to vertebrates, and they offer new evidence indicating that they are similarly distasteful or repellent to some common invertebrate predators. The widespread distribution of lycids, and their success in a wide range of predator-prey associations, would appear to be explained, in part at least, on this basis.

It would be interesting to know more about the inherent edibility or inedibility of the species associated with the lycids, since this data would enable the assemblages to be resolved into Batesian and Müllerian elements. Our own limited results are suggestive at best, and the discussion that follows is largely speculative, but might prove useful in setting the stage for further work of a more precise experimental nature.

The Pyromorphids seem to have repugnatorial properties of their own. In our experiments, the two specimens of *Seryda* used were rejected, one by a mantid, the other by a mouse. Jones (1932) and Carpenter (1921), in the experiments on birds and monkeys already cited above also found the pyromorphid, ctenuchid, and the zygaenids that they tested to be of low acceptability, and one zygaenid has been reported to have a strong odor (Marshall and Poulton, 1902). Whether odor and distastefulness are attributable to defensive secretions such as are known to occur in other moths (e.g., arctiids) remains to be determined. We made no attempt to look for secretory droplets in *Seryda*, nor did we check its odor.

None of our own trials included any of the arctiid or lithosiid mimics. There is circumstantial evidence, however, that many arctiids are distasteful and to be regarded as Müllerian elements. Arctiids are commonly aposematic, whether they are associated with mimetic complexes or not. Moreover, thoracic and tarsal glands, presumably defensive, are widespread throughout the family (Dethier, 1939; Rothschild, 1957). Jones (1932), with birds, tested two species congeneric with *Holomelina ostenta* (a presumed member of the *loripes* complex). In 14 experiments, 16 of 25 examples of *H. auriantica* Hübner were left on the trays; the other species, *H. opella* Grote, was only slightly more acceptable.

The cerambycids and the geometrid are probably Batesian rather than Müllerian mimics. *Elytroleptus* were eaten by both mantids and mice, the only predators to which they were offered. The single specimen that was left uneaten was ignored by a mouse (No. 3) that presumably discriminated against it on sight, having had previous experience with the model lycid. Many cerambycids possess noticeable odors and/or stridulate when disturbed, and this may conceivably serve in defense (Linsley, 1959). Neither species of *Elytroleptus*, so far as we noticed, had these properties. The cerambycids associated with the lycid complexes studied by Darlington (1938) and Parsons (1940) in Cuba, as already pointed out, also appear to be edible and hence are classed as Batesian mimics.

The geometrid *Eubaphe* was tested just twice, and then only with mantids, which accepted them. It appears, however, that edibility is the rule, rather than the exception, with geometrid moths. One of us (Eisner) in connection with other work has routinely fed an assortment of Eastern species to captive birds, lizards, mantids, spiders, and ants, without ever witnessing a single rejection or behavioral abnormality on the part of a predator. With few exceptions, most of the geometrids fed to birds by

Jones (1932) also had a relatively high acceptability ratio (at least those species that were tested in significant numbers). However, at least some geometrids (e.g., the Palaearctic *Abraxas*) are definitely protected and aposematic.

A number of moths other than those tested, belonging to "protected" families (Ctenuchidae, Pyromorphidae), occur widely in the same regions and environments as the lycids. They include species that may be functional members of the *L. fernandezi* or *L. loripes* mimetic complexes, or (because of an intermediate appearance) of both. Furthermore, the ctenuchid *Lycomorpha grotei*, because it has either red or yellow-brown forewings, may function as a Müllerian member of either the scarlet-winged or the yellow-winged lycid mimetic complexes, or of both, and thus may reinforce the protective effect of each.

In summary, it appears that each lycid assemblage is a composite of Müllerian and Batesian elements. The dominant form in each is a single species of lycid. This species and its sibling, together with an arctiid, and in one case (*fernandezi* group) a pyromorphid, make up the Müllerian framework of each complex, although other pyromorphid and ctenuchid moths are probably involved also. Edible longicorns, and in the *loripes* assemblage a geometrid, appear to participate as Batesian mimics. However, the division of these assemblages into Müllerian and Batesian elements according to traditional schemes should be approached with caution. In each assemblage the dominance of a single species is so strong, that the impression is given that it is the exclusive model, all other forms, Batesian and Müllerian, being subservient. The Müllerian associates (with the possible exception of *L. arizonensis*) would appear to be too scarce to contribute much on their own in the line of pattern reinforcement.

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INTERRELATIONSHIPS AND EVOLUTIONARY PATTERNS OF CELLULAR ANTIGENS IN COLUMBIDAE[1, 2]

M. R. IRWIN AND W. J. MILLER[3]
University of Wisconsin

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Previous papers from this laboratory have described the recognition of heritable antigenic characters which differentiate between pairs of species of Columbidae which hybridize. The qualitative differences which distinguish one species of a pair from the other have been obtained singly in backcross populations by mating the species hybrids and selected backcross hybrids to the other parental species. The presence or absence of these differentiating characters can be determined in related species of Columbidae by immunological tests. It is possible to determine whether such antigenic characters, when present in other species, are carried in these species as an indistinguishable or only as a similar character. For example, a previous paper (Irwin, 1953) described the sharing or non-sharing in over 20 species of Columbidae of antigenic specificities of the cellular antigens which differentiate *Streptopelia chinensis* from *S. risoria*. From such information inferences can be drawn concerning the relationships of the causative genes for the antigenic characters in the different species.

This paper describes the occurrence or non-occurrence in over 30 species of Columbidae of antigenic specificities which reciprocally differentiate *Columba guinea* and *C. livia*. Four cellular antigens (A, B, C, and E) are peculiar to *C. guinea* in contrast to *C. livia* (Irwin, Cole, and Gordon, 1936). Four antigenic characters of *livia* (A′, B′, C′, and E′; Miller and Bryan, 1953) are respectively antithetical to those of *guinea*. From observations of the reactions of different reagents for each of these characters of *guinea* and *livia* with the cells of over 30 species, inferences are drawn as to the changes that may have taken place in the causative genes for these antigenic substances during the evolution of these various species.

EXPLANATORY REMARKS AND EXPERIMENTAL PROCEDURE

Species hybrids have been obtained from reciprocal matings between *guinea* and *livia*, and backcross hybrids have been produced in successive matings to *livia* of the species hybrids and selected backcross hybrids (Irwin et al., 1936). The antigenic characters peculiar to *guinea* which have been isolated in unit form in the backcross hybrids are called A, B, C (originally designated as CD), E, and F. There has been uncertainty for several years as to whether the A and F characters were serologically distinct. Recent tests (Miller, 1953) have indicated that the A and F characters in the present colony of backcross hybrids are genetically and serologically indistinguishable. Hence in this paper their reactions will be combined under the single designation A. Other cellular antigens peculiar to *guinea* may exist, but these have not been isolated in the backcross hybrids.

A technic for the detection of each of the antigenic characters of *livia* (A′, B′, C′, and E′) has been described by Miller and Bryan (1953). Anti-*livia* serum is absorbed by the pooled cells of birds homozygous for one of the antigens of *guinea*, and the reagent so

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[3] Present address: School of Veterinary Medicine, University of California, Davis, California.

produced is reactive with the contrasting character of *livia*. The use in these absorptions of pooled cells from several homozygotes has minimized the possibility of errors in the subsequent tests which might arise because of individual differences in *livia*. Further, according to Gershowitz (1954) antigenic differences in *livia* are rarely, if ever, demonstrable at the dilution of antiserum (1:30 or 1:60) regularly used in these tests.

There were two methods of obtaining reagents specific for each of the antigenic characters of *guinea*, A, B, C, and E. One was to obtain antisera from rabbits by immunizations with the cells of backcross birds possessing any one of these characters, and then to absorb such an antiserum with the cells of *livia*. This absorbed antiserum would be a "reagent" presumably specific for the particular antigenic character of *guinea* of the backcross hybrids. The other method was to absorb anti-*guinea* serum (from rabbits) with the cells of *livia*, plus those of backcross hybrids representing three different antigenic characters of *guinea*, so that presumably the antibodies to only one specific character of *guinea* would remain in the antiserum. For example, the cells of *livia* and of backcross hybrids with antigens B, C, and E, respectively, would be expected to exhaust an antiserum to *guinea* of all antibodies except anti-A. Comparable results in agglutination of the cells of other species were usually obtained with the specific reagents obtained by either method. (This latter method has the disadvantage that if the antiserum contained antibodies to antigenic characters of *guinea* in addition to those now recognized—A, B, C, and E—such antibodies would remain after the absorptions and would complicate the results of the reactions of the reagents with the cells of other species. No evidence of such complications has been noticed.)

The cells of backcross hybrids with B, C, or E elicited antisera from which reagents specific for each character were prepared, but the cells of backcross birds with A failed to engender antibodies to A in sufficient strength to be usable in these tests. Therefore, reagents specific to A were prepared only by absorbing anti-*guinea* or anti-*picazuro* serum (*C. picazuro* contains an antigen related to A) with *livia* cells plus those of backcross hybrids with B, C, and E, as described above.

The technic of testing the blood cells of the various species of Columbidae for the presence or absence of antigenic specificities of each of the four pairs of antithetical characters of *guinea* and *livia* is essentially the same as described in a preceding paper (Irwin, 1953). The antisera to each of 24 species other than *guinea* and *livia* were analyzed for their content of antibodies reacting with the A, B, C, and E antigens of *guinea*, following their respective absorptions with *livia* cells. The specific reagents for A, A′, B, B′, C, C′, E, and E′, respectively, have also been tested for agglutination with the cells of the majority of the various species.

Further absorptions of certain of the reagents for the specific antigens of *guinea* and *livia* were made with the reactive cells of various species to determine if all or only some of the antibody specificities would be removed. If absorption by the cells of a species removed some but not all of the antibodies for a particular character, the antigen on the cells was classed as being similar to that of *guinea* or *livia*. But if the cells of another species completely removed the antibodies for a character of *guinea* or *livia*, the characters under test were indistinguishable and presumably identical in the two species. It should be emphasized that the cells of a species might completely remove the antibodies in one antiserum but not those in another by virtue of the differential response of rabbits to immunization with the cells of a species. Any statements made that the antigenic characters of two species are indistinguishable and presumably identical apply only to the results with the antisera tested, with the full realization that other antisera might or might not provide the same results.

The species used in this study belong to

several different genera; those of the genus *Streptopelia* are: *bitorquata*, also called *dussumieri*, the Philippine turtle dove; *capicola*, the Cape turtle dove; *chinensis*, or Pearlneck; *orientalis*, the Oriental turtle dove; *risoria*, or Ring dove; *semitorquata*, the African turtle dove; *senegalensis*, the Senegal or palm dove; *tranquebarica*, also called *humilis*, the dwarf turtle dove; and *turtur*, the European turtle dove. Those of the genus Columba are: *fasciata*, the band-tailed pigeon; *flavirostris*, the red-billed pigeon; *guinea*, the triangular-spotted pigeon; *janthina*; *leucocephala*, the white-crowned pigeon; *livia*, the domesticated pigeon; *maculosa*, the spot-wing pigeon; *oenas*, the European stock pigeon; *palumbus*, the European wood pigeon; *picazuro*, the Picazuro pigeon; and *rufina*, the rufous pigeon. Those of other genera are: *Caloenos nicobarica*, the Nicobar pigeon; *Chalcophaps indica*, the green wing dove; *Ducula spilorrhoa*, the white fruit pigeon; *Gallicolumba luzonica*, the bleeding heart; *Geopelia humeralis*, the bar-shouldered dove; *Goura cristata*; *Leptotila jamaicensis*, the violet dove; *Ocyphaps lophotes*, the Australian crested dove; *Phaps chalcoptera*, the bronze wing pigeon; *Phaps elegans*, the the brush bronze wing pigeon; *Zenaida aurita*, the Martinique dove; *Z. asiatica*, also known as *Melopelia leucoptera*, the white-wing dove; *Zenaidura auriculata*, the bronze-neck dove; *Zen. graysoni*, the Grayson dove; and *Zen. macroura*, the mourning dove. The blood of at least two, usually of more than two, individuals within each species has been used in these tests. Unless otherwise noted, individual differences in reactivities within the species have not been observed, but the small number of birds tested of each species does not preclude the possibility of such variation.

Representatives of these species have been purchased from various dealers in the United States or obtained as described previously (Irwin, 1953). Blood samples of individuals of two species—*C. nicobarica* and *D. spilorrhoa*—were made available by courtesy of Mr. Karl Plath, Curator of Birds, Chicago Zoological Park, Brookfield, Illinois, and of another—*G. cristata*—by courtesy of Mr. R. M. Perkins, Director, Lincoln Park Zoological Gardens, Chicago, Illinois. Mr. Plath also kindly allowed blood to be taken from representatives of *lophotes* and *guinea*.

Specific Antigenic Characters of *guinea*, in Contrast to *livia*, in Other Related Species

The respective antisera, prepared in rabbits by separate immunization with the cells of each of the 24 species other than *guinea* and *livia*, were absorbed with the cells of *livia*, and then tested with the cells of *guinea* and of backcross birds carrying, respectively, one of the antigenic characters (A, B, C, and E) peculiar to *guinea*. The results of these tests are given in table 1. The assumption in making such tests was that if a species other than *guinea* possessed a cellular antigen either identical with, or related to, one or more of the cellular antigens of *guinea* which are recognized as units in the backcross birds, antibodies to such an antigen or antigens would be present in the antiserum, and would "crossreact" with the character of *guinea*.

In table 1, it may be seen that all but one (anti-*luzonica*) of the antisera were reactive with at least one of the four unit characters of *guinea*, and only one (anti-*palumbus*) agglutinated each of the four kinds of cells with specific characters of *guinea*. Of the 24 antisera to the respective species, in addition to *guinea*, from which these reagents were made, 20 were reactive with cells carrying A, only two with cells carrying B, and 22 (but not necessarily the same 22) were reactive with one or the other of the C and E characters, or with both. According to these tests, antigens at least related to A, C, and E of *guinea* are present in the majority of the 24 species of the different genera, while B or a B-like character occurs only in two species (*oenas* and *palumbus*) of Columba.

However, these tests did not show whether the respective characters of *guinea*,

TABLE 1. *Tests of the antisera to the respective species for the presence of antibodies to the species specific antigens of* guinea *as contrasted to* livia

Antisera to	Absorbed by cells of	Reactions of the respective reagents prepared from the antisera to each of the species as given, when tested with the blood cells of the two parental species and backcross birds carrying the respective specific substances of *guinea*						Summary of the reactivities of the species specific antigens of *guinea*
		Test cells						
		livia	*guinea*	A	B	C	E	
St. capicola	*livia*	0	±	±	0	+	±	ACE
St. chinensis	*livia*	0	+	+	0	+	+	ACE
St. bitorquata	*livia*	0	±	±	0	0	±	AE
St. tranquebarica	*livia*	0	+	+	0	±	+	ACE
St. orientalis	*livia*	0	+	±	0	±	±	ACE
St. risoria	*livia*	0	+	+	0	+	±	ACE
St. semitroquata	*livia*	0	+	+	0	+	±	ACE
St. senegalensis	*livia*	0	±	±	0	±	±	ACE
C. fasciata	*livia*	0	±	±	?	+	±	ACE
C. flavirostris	*livia*	0	±	±	0	+	0	AC
C. guinea	*livia*	0	+	±	+	+	+	ABCE
C. janthina	*livia*	0	+	+	0	+	0	AC
C. leucocephala	*livia*	0	+	±	0	+	0	AC
C. maculosa	*livia*	0	±	±	0	0	?	A
C. oenas	*livia*	0	+	0	+	+	±	BCE
C. palumbus	*livia*	0	+	+	+	+	+	ABCE
C. picazuro	*livia*	0	+	±	0	+	+	ACE
C. rufina	*livia*	0	±	+	0	+	±	ACE
O. lophotes	*livia*	0	±	0	0	0	±	E
G. luzonica	*livia*	0	0	0	0	0	0	—
P. chalcoptera	*livia*	?	±	0	0	±	±	CE
P. elegans	*livia*	0	+	+	0	0	±	AE
Z. aurita	*livia*	0	+	±	0	±	±	ACE
Zen. macroura	*livia*	0	±	±	0	±	±	ACE
Z. asiatica	*livia*	0	+	+	0	+	+	ACE

Symbols: A "+" indicates varying degrees of agglutination; "±", weak but definite agglutination; "?", a questionable reaction; "0", no agglutination—at the first dilution of the respective reagents, usually 1:60.

with which the absorbed antiserum against any particular species was reactive, are present in the species as identical or only as similar characters. For example, the antiserum to *capicola* contained antibodies reactive with the cells of backcross hybrids containing, respectively, the characters A, C, and E, as is given in table 1. Further tests were necessary in order to determine the relationships of the A, C, and E characters of *guinea* to those of *capicola*. These were made following respective absorptions of an anti-*guinea* serum with the cells of *livia* plus those of each of these species, as *capicola*, and testing each such reagent with the respective cells containing A, B, C, and E to see if all or only a part of the specific antibodies had been removed. The results of such tests are given in table 2.

It may be noted in table 2 that none of the species whose cells were used in absorption removed completely from anti-*guinea* serum the antibodies for the cellular antigens B, C, and E, except that absorption by the cells of *palumbus* removed all the antibodies for C. Therefore, it may be concluded that, with this single exception, B, C, and E characters, whenever present on the cells of any of the species tested, were present only as similar, not as identical, characters. For example, the respective antisera to *oenas* and *palumbus* were reactive with the cells of backcross hybrids carrying B of *guinea*, indicating that *oenas* and *palumbus* contain

a character either identical with or only similar to B. However, since the cells of *oenas* and *palumbus* did not by absorption remove all the antibodies for B from anti-*guinea* serum, it is clear that B is not contained *in toto* on the cells of either of these two species.

In contrast, the cellular antigen A of *guinea* appears to be shared completely by some species, but in others, if present at all, it seems to be only a similar character. Thus, the cells of nine species of Streptopelia (*capicola*, *chinensis*, *dussumieri* or *bitorquata*, *humilis* or *tranquebarica*, *orientalis*, *risoria*, *semitorquata*, *senegalensis* and *turtur*) completely removed the antibodies for the A character from the anti-*guinea* serum as did those of *palumbus*, *asiatica*, *aurita*, *macroura* and probably *oenas*. In addition to the tests given in table 2, absorption of an anti-*guinea* serum by the cells of *livia* and *turtur* removed all or nearly all the antibodies for the A of *guinea*. Also, a questionable reaction for the cells of backcross birds with the A of *guinea* was noted following absorptions of anti-*guinea* with the cells of *oenas*, whose antiserum (table 1) did not contain antibodies for A. From these tests it would be inferred that, since all or nearly all the antibodies to *guinea* A were removed by the cells of these two species from anti-*guinea* serum, their cells also possess an antigenic character indistinguishable from, and presumably identical with, the A of *guinea*. Other species, whose respective antisera contained antibodies reactive with the A antigen but whose cells did not absorb all the antibodies for it from anti-*guinea* serum, were *fasciata*, *flavirostris*, *leucocephala*, *maculosa*, *picazuro*, *rufina*, and *elegans*. These results may be explained by assuming that the A character in these seven species is similar to, but distinguishable from, the A of *guinea*. Definite agglutination of A cells by the anti-*guinea* serum was noted following respective absorptions by the cells of the other three species—*chalcoptera*, *lophotes*, and *luzonica*—whose antisera did not have antibodies for the A of *guinea*.

TABLE 2. *Tests of homology or non-homology of cellular antigens in other species of Columbidae to the species specific antigens of* guinea, *in contrast to* livia

The agglutination of the test cells with *guinea* antiserum absorbed only with the cells of *livia* (column 2) or with cells of *livia* plus those of the species as listed (columns 3 to 25, inclusive)

Cells tested		*bitorquata*	*capicola*	*chinensis*	*orientalis*	*risoria*	*semitorquata*	*senegalensis*	*tranquebarica*	*fasciata*	*flavirostris*	*leucocephala*	*maculosa*	*oenas*	*palumbus*	*picazuro*	*rufina*	*lophotes*	*chalcoptera*	*elegans*	*aurita*	*macroura*	*asiatica*	*luzonica*
guinea	9	7,8	8	7,8	0	7,8	8	6,8	8	7	8	7	8	7,8	0	7,8	7,8	8	8	8	8	7,9	6,7	8
livia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	2,3	0	0	0	0	0	0	0	?	0	#	#	#	?	+	#	#	#	#	#	+	+	+	#
B	6	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	#	+++	+++	+++
C	5,6	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
E	6,7	+++	+++	+++	+++	7	+++	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Column 1	2	3	4	5	6	8																		

The digits represent the serial dilutions (doubling) at which the last trace of agglutination was visible. If the first dilution of the reagent was 1:60, 1=60, 2=120 . . . 9=15,630, etc. A ++ represents a stronger agglutination at the first dilution of the absorbed antisera than a +, otherwise the symbols are the same as in table 1.

TABLE 3. *The presence or absence in various species of Columbidae of cellular antigens similar to, or identical with, those which differentiate* Columba guinea *and* Columba livia *from each other (A, B, C and E of* C. guinea; *A′, B′, C′ and E′ of* C. livia)

Test cells	The results of teats of the blood cells of the various species with the respective reagents								Summarized phenotypes
	A of *guinea*	A′ of *livia*	B of *guinea*	B′ of *livia*	C of *guinea*	C′ of *livia*	E of *guinea*	E′ of *livia*	
Streptopelia:									
capicola	++	0	+	+	+	0	0, +	0	A BB′ C E
chinensis	++	0	+	0, +	+	0	+	0	A BB′ C E
bitorquata	++	0	+	+	+	0	+	0	A BB′ C E
tranquebarica	++	0	+	+	+	0	+	0	A BB′ C E
orientalis	++	0	+	+	+	0	+	0	A BB′ C E
risoria	++	0	+	+	+	0	+	0	A BB′ C E
semitorquata	++	0	+	+	+	0	+	0	A BB′ C E
senegalensis	++	0	+	0, +	+	0	0, +	0	A BB′ C E
turtur	++	0	+	+	+	0	0	0	A BB′ C
Columba:									
fasciata	+	0	0	?	+	0	±	0	A C E
guinea	++	0	++	0	++	0	++	0	A B C E
livia	0	++	0	++	0	++	0	++	A′ B′ C′ E′
oenas	++(?)		+		+		+		A B C E
palumbus	++	0	+	0	++	0	+	0	A B C E
picasuro	+	0					+	0	A E
rufina	+	0	?	?	+	0	±	0	A C E
Other genera:									
Chalcophaps indica	0	0	0	0	+	0	0	0	C
Gallicolumba luzonica	0	0		0	+	0	0	0	C
Geopelia humeralis	+	0	0	0	+	0	0	0	A C
Leptotila jamaicensis	++	0	0	0	0	±	±	0	A C′ E
Ocyphaps lophotes	+	+	0	0	+	0	+	0	AA′ C E
Phaps chalcoptera	+	+	0	0	+	0	+	0	AA′ C E
Phaps elegans	±	+	0	0	+	0	+	0	AA′ C E
Zenaida asiatica	++	0	0	+	+	0	+	0	A B′ C E
Zenaida aurita	++	0	0		+	0	+	0	A C E
Zenaidura auriculata	±	0	0	0	+	0	0	0	A C
Zenaidura graysoni	±	0	0	0	+	0	±	0	A C E
Zenaidura macroura	++	±	0	0	+	0	±	0	AA′ C E
Caloenas nicobarica	0	0	0		+	0	+	0	C E
Ducula spilorrhoa		0	0		+	0	?	0	C
Goura cristata	0	0	+	0	+	0	±	0	B C E

A blank indicates that the test of reagent and cells was not made. A "++" indicates that the species possesses an indistinguishable and presumably identical antigenic character to that of *guinea* or *livia;* a "+" or "±" indicates the presence of a similar substance; a "0" indicates the absence of the particular antigenic substance, i.e. the cells of the representatives of the species did not react with the particular reagent. A combination of 0 and + (0, +) indicates that the cells of some individuals of the species were reactive, those of others were not.

The digits represent the serial dilutions (doubling) at which the last trace of agglutination was visible. If the first dilution of the reagent was 1:80, 1:160, 1:320, 1:640, etc. A ++ represents a stronger agglutination at the first dilution of the absorbed antisera than a +, otherwise the symbols are the same as in table 1.

When present at all in other species, and with but one exception, three (B, C, and E) of the four cellular characters which distinguish *guinea* from *livia* were present only as similar substances. The causative genes in these species produce similar products, and may be assumed to be only similar in composition. The gene in each of the various species which produces an antigenic character indistinguishable from A of *guinea* may be assumed to be homologous to the causative gene in *guinea*.

THE OCCURRENCE IN RELATED SPECIES OF THE SPECIFIC ANTIGENIC CHARACTERS OF *GUINEA* AND *LIVIA*, RESPECTIVELY

The respective reagents for the specific characters of *guinea*, A, B, C, and E, and of *livia*, A′, B′, C′, and E′, were tested with the cells of the majority of the species of Columbidae listed in table 3. The results obtained by the use of the specific reagents for the A, B, C, and E characters of *guinea*, with but few exceptions, confirm those listed in table 1 as to the presence in the various species of antigenic characters at least similar to those of *guinea*, in comparison to *livia*. The principal exceptions noted are that the cells of each of the nine species of Streptopelia were slightly reactive with the reagent for B of *guinea* (table 3), whereas their respective antisera did not contain demonstrable antibodies to the B character (table 1). Also the cells of four species (*bitorquata*, or *dussumieri*, *lophotes*, *luzonica*, and *elegans*) were reactive with the C reagent, but their respective antisera (table 1) did not contain antibodies for the C character. It is not surprising that there was not complete agreement in the results of these reciprocal

tests, but it is puzzling that so many discrepancies were noted in the inability of the species of Streptopelia to invoke antibodies to the B character. Perhaps the species of Streptopelia possess only a "B-like" antigen which is less antigenic than B of *guinea*. Otherwise these discrepancies can be attributed largely, if not entirely, to variations in the response of individual rabbits to immunization, as has been noted for antigens peculiar to *chinensis* (Irwin and Golden, 1942).

There were four species of the genus *Columba*—*flavirostris*, *janthina*, *leucocephala*, *maculosa*—whose cells were not available for tests with certain reagents for the unit characters of *guinea* and *livia*, and which are not included in table 3. As is shown in tables 1 and 2, each of three of these four species carried characters on their cells similar to one or more of the A, B, C, and E antigens of *guinea*: AC in *flavirostris*, AC in *leucocephala*, and A in *maculosa*.

A of *GUINEA* and A′ of *LIVIA* in Other Species

There were four species—*cristata*, *indica*, *luzonica*, and *nicobarica*—of those listed in table 3, whose cells were not reactive with the reagents for either A of *guinea* or A′ of *livia*. The cells of four other species—*chalcoptera*, *elegans*, *lophotes*, and *macroura*—were agglutinated not only by the reagent for A′ of *livia*, but also by the reagent for A of *guinea*. In contrast, the cells of 18, possibly 19 (including *oenas*), species other than *guinea* were agglutinated only by the A reagent. Of these, 14 (adding *jamaicensis* to the species with characters presumably identical with A of *guinea*) contain a character which in these tests was indistinguishable from the A of *guinea*, and nine carry a character that is only similar to it (see also table 2). These numbers do not include *oenas* (tables 1 and 2) whose cells probably contain A as a character indistinguishable from the A of *guinea*, but do include several species not listed in tables 1 and 2. There are nine species of Streptopelia, two of Columba besides *guinea* (*palumbus* and probably *oenas*, as given in table 2), two of Zenaida (*aurita* and *asiatica*), one of Leptotila and one of Zenaidura (*jamaicensis* and *macroura*) which contain A apparently *in toto*. On the assumption that the gene for A in these 15 species is the same as in *guinea*, this character represents one peculiar to *guinea*, in contrast to *livia*, whose causative genes are shared by *guinea* and these 15 species. These observations confirm and extend a previous report (Irwin, 1938) which showed that the A of *guinea* was shared with *chinensis* and *risoria*.

At least two antigenic specificities may be postulated for the A character. One of these, but not necessarily the same specificity, is present in each of the nine species with a character similar to A. The second specificity must be postulated to explain the difference between each such related character and the A of *guinea*. Unfortunately, peculiarities in the reagent for A did not permit an analysis of the similarities and dissimilarities among these A-like characters in the nine species.

The results of tests to determine whether the antigenic specificities in the cells of the four species (*lophotes*, *chalcoptera*, *elegans*, and *macroura*) reacting with the antibodies of the A′ reagent are alike or dissimilar are given in table 4. It will be noted that absorption of the reagent for A′ by the cells of *macroura* removed antibodies only for themselves, and that similar absorptions by the cells of *lophotes*, *chalcoptera*, or *elegans* removed antibodies for the cells of one another but not for those of *macroura* nor for those with A′ (*livia*). A combination of the cells of *macroura* and *lophotes* did not exhaust the reagent of antibodies for A′ cells, so at least three specificities are required in the reagent to explain the results of table 4—one specificty reactive with the cells of *macroura*, another common to those of *lophotes*, *chalcoptera*, and *elegans*, and a third peculiar to cells with A′—implying at least three antigenic specificities in the A′ character corresponding to those of the antibodies in the reagent. The genetic implica-

TABLE 4. *Tests for the specificities of antibodies to the A′ substance of* Columba livia, *in contrast to* C. guinea, *as revealed by the reactivities of the reagent for A′ following absorptions with the cells of various species*

Test cells	Agglutinations of the test cells by an anti-*livia* serum (No. 143S2) absorbed only by the blood cells of backcross hybrids homozygous for the genes for A (*A/A*), or in combination with the cells of species as listed:					
		chalcoptera	*elegans*	*lophotes*	*macroura*	*lophotes*[1] and *macroura*
Backcross hybrids (*A/A*)	0	0	0	0	0	0
C. livia	+	+	+	+	+	+
P. chalcoptera	+	0	0	0	+	0
P. elegans	+	0	0	0	+	0
O. lophotes	+	0	0	0	+	0
Zen. macroura	+	+	+	+	0	0

Symbols: Same as in table 3.

[1] Parallel results were obtained following the absorptions by the cells of *macroura* and *chalcoptera*, and of *macroura* and *elegans*.

tions of these findings will be considered later.

B OF *GUINEA* AND B′ OF *LIVIA* IN OTHER SPECIES

The data of table 3 show that the cells of the nine species of Streptopelia were reactive with the reagents specific for B and B′, respectively. In other genera, only three species (*palumbus*, *cristata*, and *oenas*, see table 1) other than *guinea* showed evidence of the presence of B or a B-like character, and only *asiatica* showed evidence of the presence of B′ or a B′-like specificity. With but few exceptions, the cells of individuals within each of the nine species of Streptopelia were agglutinated by both B and B′ reagents. However, individual differences were noted in two species (*chinensis* and *senegalensis*) in that the cells of one of 16 *chinensis* and two of 54 *senegalensis* were not agglutinated by the B′ reagent, and therefore seemingly did not possess a B′-like substance. There were several individuals of *chinensis* and *senegalensis* whose cells were agglutinated only weakly by this reagent, whereas those of the others within each species were strongly agglutinated in the same test. These weakly reacting cells may be explained (a) by peculiarities of the technic, (b) by the assumption that they reflect effects of gene "dosage" as described in cattle by Stormont (1952), or (c) by the assumption that there exist within the two species two kinds of alleles producing B′-like characters. The cells of all individuals tested in these two species (16 *chinensis* and 54 *senegalensis*) were agglutinated by two of three B reagents, so that individual differences in each species might be expected by virtue of the presence or absence of one or more B′-like specificities.

The tests made to determine whether the specificities of the B character in the various species of Streptopelia were identical with or only similar to the B of *guinea* were not completely satisfactory, in part because one of the reagents used (from three antisera to B) appeared to have lost its reactivity with the cells of *chinensis* and *senegalensis*, and in part because some results in agglutination following the respective absorptions were very weak. However, according to the differential reactivities of the cells of the several species, as given in table 5, following the absorptions as listed, there are at least three antigenic specificities of the B of *guinea*. Two of these are required to explain the differences between *risoria* and *semitorquata*, and the third to explain the differences of BB or BB′ cells from both these species.

Absorptions of the B′ reagent (anti-*livia* serum exhausted of all antibodies except those for B′ by the cells of backcross hybrids

TABLE 5. *A summary of tests of the cells of various species of Columbidae for similarities of the antigenic specificities to the B substance of* C. guinea, *in contrast to* C. livia

Test cells	Agglutination of the test cells with one or more of three anti-B sera, following absorption by the cells of *livia* or by the cells of *livia* plus those of the species as listed:						
	—	*capicola*	*tranquebarica*	*orientalis*	*risoria*	*semitorquata*	*rufina*
capicola	+	0	0	0	0	0	
chinensis	?						
tranquebarica	±	0	0	0	0	0	+
orientalis	±	0	?	0	0	0	+
risoria	+	±	±	0	0	±	+
semitorquata	+	0	?	0	±	0	
senegalensis	±			?	±		±
turtur	+,0	0	0	0	0		
guinea	++		++	++	++		++
livia	0	0	0	0	0	0	0
rufina	?		0	0	0		
BB or BB′	++	++	++	++	++	++	++

Symbols: Same as in tables 1 and 3.
The test cells labelled BB or BB′ were taken from backcross hybrids, as described in the text.

homozygous for the gene for B) by the cells of *asiatica* removed antibodies only for the cells of this species. The antigenic factor in *asiatica* corresponding to these antibodies may be called B′a. Separate saturations of the B′ reagent with the cells of *chinensis*, *dussumieri* (*bitorquata*), *humilis* (*tranquebarica*), *risoria*, *semitorquata*, *senegalensis*, or *turtur*, resulted in the removal of antibodies for the cells of each species and for *asiatica*, but not for those of *livia* or the backcross hybrids with B′. Hence these species of Streptopelia possess the "a" specificity of *asiatica*, and at least one additional specificity "b." Further, the B′ character in *livia* and in the backcross hybrids must have the specificities "ab" and at least one more, "c," to account for the differences in reactivities of the cells of *livia* and the backcross hybrids with B′ from those of the various species with either "a" or "ab."

THE C CHARACTER OF *GUINEA* AND THE C′ CHARACTER OF *LIVIA* IN OTHER SPECIES

Except for its absence in *livia*, the C character of *guinea* was found in all but one of the 29 species tested and this species (*jamaicensis*) was the only one whose cells were faintly but definitely reactive with one of seven reagents for C′ (table 3). Since the reagents for C′ were reactive with *livia* cells at high dilutions (1:480 to 1:30,720), the lack of their reactivity with the cells of the various species indicates strongly that a character serologically closely related to C′ is very rarely present in species other than *livia*. In contrast, *palumbus* appears to possess the C of *guinea in toto* on its cells, while the other species possess only C-like characters. Bryan (1953) has reported that the C antigen of *guinea* has multiple specificities, as revealed by the likenesses and dissimilarities of the C-like characters in the various species. The details and implications of his findings will be discussed elsewhere.

THE E OF *GUINEA* AND E′ OF *LIVIA* IN OTHER SPECIES

One or more of many specific reagents for the E of *guinea* (including 10 reagents for E reported in 1947 by Jones) were reactive with the cells of eight of the nine species of Streptopelia, of four species (five with *oenas*, table 1) of Columba other than *guinea* and *livia*, and of 10 of 15 species in other genera. (In addition to the tests listed in table 3, several E-reagents were tested (Jones, 1947) with the cells of *C. flavirostris* (see table 1) but without any reactivity, and three of eight reagents for E agglu-

tinated the cells of representatives of *Leptotila verreauxi*.) The only reactivities of any of three reagents for E′ of *livia* were with the cells of *livia*, and, of course, with all backcross hybrids heterozygous for the gene for E of *guinea*.

As is shown in table 3, out of 30 species there were 22–23 other than *guinea* with E or an E-like character, none with E′ other than *livia*, and five, possibly six (*turtur*, *indica*, *humeralis*, *luzonica*, *auriculata*, and possibly *spilorrhoa*), in which no character related to either E or E′ was demonstrated. According to the findings of Jones (1947), there were multiple specificities of the E character in various species. These previous findings are being re-examined and extended, and will be presented elsewhere.

Discussion

If one assumes a common ancestral form for the species represented in these tests, it appears reasonable to presume that there would be more antigenic specificities which are shared by any two of these species than which differentiate them. Presumably this is a reflection of the various degrees of relationship of the genetic material responsible for such specificities. Thus, the cellular antigens could be indistinguishable and presumably identical in both species, or only similar, as has been described above in related species for the antigens which differentiate *guinea* and *livia*. Buchbinder (1934) described the appearance of a cellular antigen, in presumably homologous form, in many species of the class Aves, including several species of Columbidae which were tested in the present study. (This antigen was related to one which occurred in some species of Pasteurella.) Other antigenic characters which are shared in whole or in part by the species included in the present study have rarely been recognized as single characters, but many undoubtedly exist. For example, previous results (Irwin and Cumley, 1943) have indicated that neither *guinea* nor *palumbus* shares cellular antigens with *livia* which are not also shared with each other. Further, two (A and C) of four of the antigenic substances which distinguish *guinea* from *livia* are shared presumably completely with *palumbus*, the other two (B and E) are shared only in part, thus indicating a closer relationship between *guinea* and *palumbus* than of either with *livia*. This is another example of how two species may share antigenic characters which differentiate each of them from a third species. (Insofar as these antigenic relationships have pertinence as a criterion for taxonomic purposes, these data are not in agreement with the classification of the species of Columba proposed by von Boetticher (1954).) Such antigenic characters, whether present as identical or as related antigens, would be responsible for the absorption of the antibodies when the antiserum against one species is mixed with the cells of another. Examples of the results obtained in such comparisons among species of Columba have been given by Irwin and Cumley (1943).

Some antigenic characters which differentiate each of the two species, *guinea* and *livia*, from each other have been recognized and the behavior of these differentiating characters has been observed in the backcross populations. Each pair of contrasting antigenic characters (A and A′, B and B′, C and C′, E and E′) of these two species has behaved in the common genetic background of the backcross populations as expected if the causative genes were alleles (Miller, 1953; Miller and Bryan, 1953). (Spencer (1949) proposed that genes behaving in this manner would be defined as homologous genes.) However, if two or more linked genes produced one or more of these contrasting pairs, the probable relationships among the causative genes in the various species would be expected to conform to the pattern described elsewhere (Irwin, 1953).

The test fluids, or reagents, which reacted with the differentiating antigenic characters of *guinea* and *livia*, respectively, were used in testing the cells of related species for the presence or absence of characters identical with, or related to, the four pairs of contrasting characters. In general, the reactiv-

ities of the cells of the various species of Columbidae toward the respective reagents were as expected if the respective pairs of characters of *guinea* and *livia* were also antithetical in these related species. That is, the cells of a majority of the species possess only one or the other of the antithetical characters, usually as a similar character, while the cells of a minority of the species (a) possess antigenic specificities related to both members of a pair of contrasting characters (A and A′ or B and B′), or (b) possess no demonstrable antigenic character related to either of a pair of antithetical characters of *guinea* and *livia*. Only rarely was a character which differentiated *guinea* from *livia* present presumably in indistinguishable form in another species—15 with A and one with C—and no species of those tested possessed in indistinguishable form an antigenic character differentiating *livia* from *guinea*. In fact, the specific substances of *livia*, as detected in these tests, were much less widely distributed in the various species than were those of *guinea*.

A somewhat comparable distribution in related species of genetic characters which differentiate *Drosophila americana* and *D. virilis* has been summarized by Patterson and Stone (1952) from the reports by Spencer (1938, 1940a,b) and Stalker (1942). The red color of the pupae of *americana*, rather than gray or black, and the relative resistance of *virilis* to anesthetization with ether in contrast to the susceptibility of *americana*, are two of the characters which differentiate the species from each other and also from other members of the group.

Glenny and Amadon (1955) describe unusual characteristics of the New Guinea pigeon *Otidiphaps nobilis* which seem to justify subfamily status, setting it apart from other pigeons much as the *livia* antigenic traits seem to set *livia* apart from other pigeons. These unique and distinctive features of *Otidiphaps nobilis* include greatly reduced furcula, broad rostrum sterni, unusual origin of the coracoid major artery, presence of two coracoid minor arteries, absence of a ligamentum botalli, 20–22 tail feathers, and posterior tarsal scutes. However, these authors believe such traits should be used as an indication of variability in the Columbidae of a degree to justify suppressing the Göurinae and the Didunculinae, leaving two large subfamilies.

It is peculiar that the species whose cells possessed demonstrable characters related to those specific to *livia* are not species of the genus Columba. That is, the antigenic specificities which differentiate *livia* from *guinea* are among those which also distinguish *livia* from the majority of the other species tested. The much wider distribution in these species of antigenic characters related to those specific to *guinea* than to those specific to *livia* suggests that the causative genes for the four antigens peculiar to *guinea* are more closely related to and consequently less divergent from the genes of an ancestral species than are the genes for specific substances in *livia*.

There were only four of the species listed in table 3 in which a character related to A′ of *livia* could be demonstrated, nine with a character related to B′, one with a C′-like and none with an E′-like character. According to the analysis of the specific components of *livia*, not present in *guinea*, as previously reported (Irwin and Cumley, 1943), three (*fasciata*, *picazuro*, and *rufina*) of the four species of Columba included in this report should share components of one or more specific antigens with *livia* to the exclusion of *guinea*. Parallel observations (unpublished) were made on the cells of two species (*chalcoptera* and *lophotes*) with the reagent for the specific antigens of *livia*. Whether the one or more characters in these five species are related to, or are additional to, those recognized as peculiar to *livia* (A′, B′, C′, and E′), in contrast to *guinea*, is not known.

The distribution in the various species of the antithetical characters of *guinea* and of *livia*, A and A′, may be compared with that of the A and B antigenic factors of man in related species. Thus, according to Land-

steiner and Miller (1925a), the A and B factors as they appear separately or together on the blood cells of anthropoid apes (chimpanzee, gibbon, and orang) are indistinguishable from and presumably identical with those of human blood, implying homologous genes for either A or B substances, as they appear in the species. However, in tests involving 36 species of lower monkeys, these authors (1925b) found that 12 species of New World monkeys (Platyrrhina) and six species of the genus Lemur possessed on their cells a character related only to the B of humans, and no factor related to either A or B was detected on the cells of 18 species of Old World monkeys (Cercopithecidae). From these findings it would be reasonable to conclude that the respective genes in man for either A or B, or both, are shared with one or more species of anthropoid apes, and that some species of lower monkeys contain a gene with an effect only similar to that of the gene for B in man. The wider distribution in species of primates of the B than of the A character of human cells is somewhat comparable to the wider distribution in Columbidae of the A of *guinea* than of the A′ of *livia*.

If single genes in *guinea* and *livia* are responsible for the respective antigens specific to each species, the relationship of the genes in one species to those producing similar antigens in the other species of Columbidae could be satisfactorily explained by assuming a multiple series of alleles with related effects and presumably with multiple antigenic specificities because of the observed cross-reactivities. But if two or more linked genes produce the respective antigenic characters specific to *guinea* and to *livia*, the probable relationships of these genes in the various species would theoretically become more complex. Such potential relationships have been discussed elsewhere (Irwin, 1953).

There were many species whose cells did not possess either of one or more pairs of these contrasting substances (chiefly B and B′). The alternative explanations for this situation might be (a) that mutations in the evolution of these species had resulted in end products which were no longer cross-reactive with the present reagents detecting the antigens of either *guinea* or *livia*, or (b) that such a gene had been lost during the evolution of the species. The authors prefer the first alternative, but recognize that both explanations may obtain among the species tested. Assuming the first alternative to be true, these tests might well provide examples of the statement by Dobzhansky (1941) that "Divergence of evolutionary lines . . . probably involves . . . a gradual increase of the differences between the structure of the genes which had been identical or similar in the ancestral forms."

The cells of a few species were observed to possess antigenic substances related to *both* members of a pair of antithetical characters. Thus, *lophotes*, *chalcoptera*, *elegans*, and *macroura* (*macroura* carries A *in toto* and an A′-like character) contained cellular substances related to both A of *guinea* and A′ of *livia*, while the nine species of Streptopelia had antigenic specificities related to both B of *guinea* and B′ of *livia*. However, since some individuals of *chinensis* and *senegalensis* lacked the B′ specificity but carried the B, one must assume that these antigenic specificities in these two species are controlled by at least two genes—(a) one for the B-like specificity and the other for the B′-like specificity, or (b) one producing a B-like product and another producing both B-like and B′-like effects. A parallel explanation may account for the seven species of Streptopelia in which no individual differences in their content of B- or B′-like substances were observed. Another possibility is that these seven species are homozygous for a gene which produces the combination of B- and B′-like specificities. This situation would parallel the report by Wiener (1938) that the blood of chimpanzees possessed specificities related to both M and N of human cells, presumably the product of a single gene. (Recent findings (Levine et al., 1955) indicate that the blood cells of chimpanzees may contain M-like and MN-like factors, rather than only an MN-like factor.) On the

assumption that the antigenic products of allelic genes are more similar than dissimilar, whereas only the differences are readily detectable, it would not be unexpected that a single allele in another species could have an antigenic effect related to the differentiating specificities which are produced separately by a pair of alleles within a species.

A pertinent finding resulting from this assay of the evolutionary changes of the antigenic characters of the blood cells of the species of Columba, and of their causative genes, is that the other species of Columba which were tested, with but two exceptions, do not possess any of the differentiating antigenic characters of *guinea* and *livia* in indistinguishable and presumably identical form. The A of *guinea* is probably homologous in *oenas* (table 2), as are the A and C characters in *palumbus*, whereas A, B, C, and E of *guinea*, if present in *fasciata*, *flavirostris*, *leucocephala*, *maculosa*, *picazuro* or *rufina*, are only similar characters. In contrast, the A of *guinea* appears to be contained in identical form in the nine species of Streptopelia, and in some species of three other genera. Within the genus Columba these relationships correspond to previous observations (Cumley and Irwin, 1944) that the species of Columba of the Old and New Worlds comprised two antigenic groups. (*Guinea*, *oenas*, and *livia* are species of the Old World, *fasciata*, *flavirostris*, *leucocephala*, *maculosa*, *picazuro*, and *rufina* of the New World.) Further, since the Streptopelia are Old World species, one could hypothesize that species of related genera might—but need not—tend to follow a similar pattern in association of antigenic composition and geographical range. Any such relationship is only incidental, however, because four species—*asiatica*, *aurita*, *jamaicensis*, and *macroura*—of the New World carry A of *guinea* seemingly *in toto*.

The cellular antigens of *guinea*, in contrast to *livia*, are related to those in species from widely scattered areas of the globe. In contrast, only four species—three from Australia (*lophotes*, *chalcoptera*, and *elegans*) and one (*macroura*) from North America—possess antigens related to A′ of *livia*, and ten species—nine from the Old World and one (*asiatica*) from North America—carry characters related to B′ of *livia*. By this criterion the Old World species, *livia*, is much less cosmopolitan in the distribution of its specific gene effects than is the contrasting species of the Old World, *guinea*. The changes which have taken place in the genes producing cellular antigens on four of the chromosomes of these two species, *guinea* and *livia*, in relationship to those of an assumed common ancestral stock, have seemingly been much more marked in the evolution of *livia*. That is, *livia* is set off much more than *guinea* from the other species of this study since only rarely do any of these species possess a substance of the blood cells specific to *livia*. In contrast, the genes which effect antigenic differences of *guinea* from *livia* are present in other species, occasionally as homologous genes, but generally as genes with similar rather than identical effects. It is assumed that such genes form a multiple allelic series.

Summary

Over thirty species of Columbidae have been tested for their content of cellular antigens which distinguish *C. guinea* and *C. livia* from each other. Three (A, C, and E) of the four cellular antigens (A, B, C, and E) of *guinea* are widely distributed in these species, occasionally as characters indistinguishable from those of *guinea*, but usually only in similar form. The B antigen of *guinea* is less widely distributed than the other three characters, implying that B sets *guinea* apart from other species to a greater extent than do any of the other three antigens. The four cellular antigens possessed by *livia* but not by *guinea* were rarely present in the other species even as similar, never as identical, characters. None of the specific characters of *livia* were demonstrable in five other species of Columba.

Undoubtedly the relationships of the cellular antigens in these various species are an index of changes in the causative genes, so that the relationships among the cellular

antigens are indicative of the changes from a common ancestral form which have occurred in the evolution of these species.

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ECOLOGICAL ASPECTS OF FLOWER EVOLUTION. II. ZOOPHILOUS FLOWER CLASSES[1]

L. VAN DER PIJL

Rijksherbarium, Leyden

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For a century botanists have tried to construct schemes to classify flowers apart from taxonomy. As quite a number of parameters (forms, diverse functions, visitors) had to be reckoned with, all the systems are more or less one-sided.

Werth (1915, 1956) objected to the vagueness of Delpino's ecological classes (according to pollinators), which "only comprise the extremes" and pointed to their structural diversity. He therefore promoted the use of structural types (*Bautypen*) of a supposed autonomous, morphological nature and showed the emerging of higher types during geological periods.

What is pure form to one man is, however, crystallized function to another. The structural types are not independent of pollination, as shown above (cf. Leppik), and as admitted incidentally by Werth.

The exclusive use of "morphological" types, according to the way of pollen deposition, splits natural entities and leaves some clear and natural ecological classes in the cold. Therefore, Werth has to discuss hydrophiles, anemophiles, pollen flowers, sapromyophilous traps, etc., separately in a large part of the book. The convergence in sapromyophilous flowers is ascribed (p. 92, 123) to "*einem zielgerichteten Schöpfungswillen*" (finalistic creation).

Here I will try to revive interest in the classes according to the visitors—classes with bad boundaries, but with a clear center, foci of differentiation in different substrata but leading to convergence, a style. Acquaintance with them may shed light on evolutionary processes in the past and peculiar forms in the present. I shall, of course, not try to give a complete review but shall make a selection in the direction of dynamics.

[1] Part I of this series appeared in EVOLUTION, v. 14, no. 4 (1960).

CANTHAROPHILY (POLLINATION BY BEETLES)

The main points (mostly negative) have been discussed already: often pollen or food bodies or traps for attraction; nectar (when present) open; few optical attractions; no special shape; no depth effect; no nectar-guides; the strong odor sometimes fruity, sometimes aminoid. Sometimes we find large single flowers (class 5 of Delpino), sometimes cylindric or flat complexes of small flowers fit for poor flyers (class 6 of Delpino).

Jaeger (1957) wrote in his review (p. 394), obviously acquainted with European mixed cases only: "There are no beetle flowers." One might rather say: The flower is fundamentally a beetle flower and many have remained so or have become so.

We may dispute whether in the cantharophilous flower-complexes of *Cornus*, *Spiraea*, *Viburnum*, *Sambucus*, Umbelliferae, Proteaceae, etc., the cantharophily is primary or secondary. That flies are often found on them is no wonder—as I said before.

The flat complex of Compositae, dating from early Cretaceous, later became ecologically backward, but is now in progression. Some of them (*Brachyglottis-Adenostyles-Cenia* and *Wyethia* species and many others in South Africa), and to a lesser degree *Tanacetum* and *Achillea* are still cantharophilous. Vogel (1959) paid little attention to beetles (no *Stil?*) but said (p. 77) that beetles are important on the masses of annual Compositae in South Africa.

In some Proteacae we also find open complexes with beetles (*Leucadendron decorum*, *Protea scolymocephala* and *Pr. mundtii*, all more or less cantharophilous according to Marloth (1913-1925).

In New Zealand, beetles (together with flies) are the dominant flower insects, as

described by Thomson (1927) and Heine (1938). There may be depauperization as well as primitivity in this condition.

Dr. Grant wrote me that in California all *Calochortus* species, all Cactaceae, *Eschscholtzia* and some other Papaveraceae and some *Rosa* spp. are pollinated by Nitidulidae and Melyridae. *Cuscuta* there is also beetle-pollinated (weevils).

A promising field exists in the tropics for studies of beetle pollination.

Sapromyophily (Pollination by Carrion and Dung Flies)

A general class of fly-flowers would be poorly distinguished as some of the higher Diptera are as specialized as the Apidae. I should like to consider the flies that are not eutropous pollinators and have coprophilous tendencies. Though this group is very heterogenous, with transitions to flower preference, it seems to have evoked the origin of a distinct flower class. It is now a peripheral, convergent group of the most divergent taxonomic origins. Just as in beetle-traps the connection with allotropous flies still means irregular pollination. I have found strong variations in the numbers of visitors, apparently dependent on the presence of breeding-substrata for the flies.

The ecological, recent nature of sapromyophilous adaptations is especially clear in the orchids. There an organization built strictly for bee pollination had to use the strangest detours and reorganizations (to be described below) to make the flowers fit to deceive much lower pollinators.

In the Asclepiadaceae there exists, perhaps, some bond with a pre-existing or even persistent organization fitted for flies, since here the sapromyophilous type occurs in many different genera. Good presents this as "autonomous repetition." He even points to the "repetition" of such character combinations inside this family in the Araceae and in *Aristolochia*—where they represent sapromyophilous characters and are clearly parallel adaptations.

The angiospermous families strongly affected by sapromyophily are: Asclepiadaceae, Aristolochiaceae, Sterculiaceae, Rafflesiaceae, Hydnoraceae, in the Monocotyledons the Taccaceae, Araceae, Burmanniaceae, and, of course, the versatile Orchidaceae as a regression. For the curious case of *Theobroma* (pollinated by a *Forcipomyia*) see Soetardi (1950) and Posnette (1950).

It is curious and perhaps a mark against myophily as generally primitive that in the Ranales sapromyophilous flowers are rare. Perhaps cadavers and dung (of reptiles) and also ancestral flies were different. Some Annonaceae show it: thus species of *Polyalthia*, *Sapranthus*, *Asimina*, and *Duguetia* (see also *Mitrephora*, discussed below). The primitive lantern-construction (see below) of some annonaceous flowers points perhaps to a more general trap design for beetles and non-coprophilous flies. See also the lantern-type of *Hydnora* in Vogel (1954, pp. 78, 191).

In the Rafflesiaceae, Hydnoraceae, and Aristolochiaceae the trapping of flies and beetles may nevertheless perhaps be used as a flower-ecological aspect to confirm the bonds with ancestral Ranales. In the Araceae too fly-flowers are often separated only vaguely from beetle-flowers.

The differential characteristics of this class as shown by comparative morphological study (cf. van der Pijl, 1953, and Vogel, 1954) are: (1) radial shape without nectar-guide; (2) purple-brown or greenish color; (3) often no food, sometimes open nectar or pseudo-nectaries; (4) transparent parts to be designated as light windows; (5) smell of decaying substances; (6) often lantern type by fusion of petal tips, with lateral apertures between, to be designated as "slits"; (7) in traps a ventricose lower part ("kettle") with arresting devices; (8) mobile appendages, the "*Flimmerkörper*" of Vogel, or fluttering petals; (9) filiform appendages, the so-called "tails."

Any "*Ausnützung*" (incidental utilization) of loose characters, though probable in the initial phases, is out of question for most cases. The syndrome is strongly correlated and the elaborative development well di-

rected. The type described as "*Ekelblüten*" in Europe is mostly but a poor shadow.

The morphological nature of one character, the "tails," varies from case to case. We find: sterile bracts (*Tacca*), petal tips (*Theobroma*, *Trichosacme*, *Cypripedium* spp.), calyx- or perigone-tips (*Aristolochia*, *Masdevallia*, *Sterculia*), spathe tips (*Arisaema* spp.), appendix tip (*Arisaema* spp.). See Troll (1928) and van der Pijl (1953).

The strong convergence has struck many early authors. Goebel explained the lantern-construction as due merely to an arrest in bud-development and ridiculed the tails. Troll (1928) thought that this criticism and some incomplete experiments (mentioned before) had done away with any ecological explanation. It was all "*Gestalt*." He originally admitted significance for the odor (which he obviously could not place in his "*Gestalt*") and later for the light-windows.

The improbability of "*Gestalt*" becomes more obvious when we see that entirely different organs having connections with flies, like the pitcher-leaves of insectivorous plants, have the same convergent adaptations. Hallier (1897, p. 752) already pointed to this convergence, even in coprophilous and fly-dispersed mosses (*Splachnum*) and the fruit-bodies of Phallineae like *Dictyophora*. Vogel (p. 33), though refuting such likenesses as just "*Ausnützung*" and recognizing the ecological significance, maintained it as "*Stil*."

The predominance of myophily in African desert plants is striking. In those regions flies are important. It is, however, also striking that in the Cactaceae there is no clear old or present fly-phase. Is this a consequence of differences in the fauna or structure or phase?

In sapromyophilous orchids like *Bulbophyllum*, *Cypripedium*, and *Pterostylis* the refined traps with irritability and a catapulting labellum, etc., are not to be considered as just catching traps comparable with *Aristolochia*, but as devices to guide unintelligent flies to the stigma of a precision flower. Sargent (1909) gave a fine analysis of *Pterostylis* and Werth (1956, pp. 81–92) also discussed this wonderful flower. Some orchids, like *Stanhopea*, even force bees (*Euglossa*) in this way (Pohl, 1927). In such traps there is no protogyny and no long imprisonment.

In these orchids the labellum has lost its original function. In *Masdevallia* it has mostly become functionless; here we have a flower returned to the radial shape of some *Aristolochia* species, often even with sympetaly.

A digression for taxonomists: Is the orchid *Cryptophoranthus*, otherwise a *Masdevallia*, to be considered as a separate genus just on account of its queer fused sepals? The answer seems to be no. The lantern of this fly-flower lies within the range of the syndrome, so well represented in *Masdevallia*.

The same relates to *Cirrhopetalum* as apart from *Bulbophyllum*. Its tails, fringes, slits between fused petals, its return to radial inflorescences, are just further myophilous refinements. This seems morphology in the making—just as in the beetle- and fly-era millions of years ago.

In some groups the general myophilous complex seems already suprageneric, though there is also narrow specialization. It is curious that in the orchids ecological barriers replace the sterility barriers so weakly developed here. The strong speciation in polymorphous giant genera like *Cypripedium* sens. lat., *Masdevallia*, *Bulbophyllum* and related genera may be correlated with a strong specificity of odors and of pollinators. The same may be true in the large genus *Pterostylis*, where each species has its own dipteran (Sargent, 1909). The convergence of this orchid with some Araceae is extremely striking; along with the case of *Masdevallia*—*Aristolochia* this is a warning against "*Bautypen*."

One more instance of the importance of ecological insight for taxonomists may be added to what has been said already on the Annonaceae. The instance is drawn from the study of Sinclair (1955). His figure 4 shows a nice range of development in the

direction of the lantern-flower of Mitrephorae. The functional aspect of these traps for beetles and flies is left aside. The coloring of some *Pseuduvaria* and *Mitrephora* flowers, however, suggests sapromyophily. The early basal sympetaly of some species (of *Papualthia*, *Hexalobus*, *Cardiopetalum*, etc.), leading to a "kettle," might be added to the picture. The strong convergence to *Aristolochia*, *Ceropegia*, and some Sterculiaceae then becomes interesting.

Melittophilous Subclasses (Pollination by Bees)

We have already discussed bee-flowers in general. The Papilionaceae, Labiatae, and Orchidaceae bear the imprint of the hymenopteran clearly in their lack of red; in the frequency of color contrasts; their intricate, closed, zygomorphic flowers; the scarce nectar (hidden, but not deeply); the nectar-guide; and the alighting place.

To return to Darwin and his classical red clover, a trifling change has indeed appeared to be important in the switching over from *Bombus* to *Apis*. Modern races of the honey bee with slightly longer mouthparts are nowadays rather frequent on *Trifolium pratense* in Europe. In New Zealand too the introduced *Bombus* is no longer the all-important pollinator. *Apis* now pollinates 90% of the flowers there, perhaps for the same reason (Forster and Hadfield, 1958).

Vogel (1954, p. 44) confirmed for South Africa the class with micromelittophily, abundant in the heathes and savannas. The small flowers stand on stiff filiform stalks spreading horizontally. They remain hidden between the low vegetation but vibrate easily and seem in this way to attract small Hymenoptera in this biotope.

A contrasting group is that of the bumblebee flowers. As a later specialization with quantitative refinement of heterogenous forms they are morphologically badly demarcated. An extreme of this group are the tropical flowers more or less exclusively pollinated by *Xylocopa* spp., the big and rude carpenter bees, that make boreholes in wood with their strong mouthparts.

I found (1954) many instances among orchids and some large-flowered Papilionaceae (*Canavalia*, etc.). Besides the characteristics of very large nototribe bee-flowers we find firstly an extra strong lock-out, with mechanical reinforcement of the alighting place. In the Papilionaceae the latter feature is furnished by the resupinate thick standard. The significance of this specialization has been proved experimentally. The flowers obtain a striking convergence with the large Labiatae. This demonstrates that a "*Fahnenblume*" can easily be transformed into a "*Rachenblume*," and that the morphological types are not as primary as Werth thinks.

Burkart (1937) described the opposite case, where a usually nototribe labiate changed into a sternotribe, explosive "*Fahnenblume*" imitating a member of the Papilionaceae.

The wonderful flower of *Thunbergia grandiflora* is narrowly adapted to the largest *Xylocopas*. Its extra-floral nectaries lure masses of ants, guiding them to the flower base. The flower is never visited by other insects and never robbed. In some *Ipomoea* spp. I could prove experimentally the protective value of the ant-guard against robbing.

The carpenter bees puncture the less adapted flowers easily, even more than *Bombus* does in Europe. This dangerous side-effect is, however, balanced in the adapted tropical flowers, sometimes by the ant-patrol, sometimes by mechanical reinforcement of the flower base. I point to this specially because of Melin's remarks that selection has produced no protection against puncturing by hummingbirds. The situation involving *Bombus* in Europe is evidently still unbalanced.

Sphingophily (Pollination by Hawkmoths)

The characteristics of the flowers are correlated with those of the Sphingidae. The plate of Vogel (1954, pl. III) shows this.

Odor heavy-sweet; color whitish or absent (green); form not necessarily zygomorphic; mostly with narrow tube or spur; rim often turned back, no place for alighting; nectar abundant; anthesis nocturnal; anthers often movable; deep dissection. The type is less frequent outside the tropics.

The odor is quite typical and seems to act directly, not just as a signal based on experience, whereas it is not interesting for other insects.

Though the type develops most easily in higher sympetalous families, it is found in a single Ranalian and frequently in Cactaceae and Capparidaceae. The differentiation in most families seems peripheral, mostly intrageneric, also in orchidaceous genera, perhaps deeper in the Cactaceae.

Sphingophily is essential in Capparidaceae, where it seems to have put a general stamp on the flowers, though there are many deviations. A simple, radial pollen-flower of the Papaver-type has become a nocturnal brush-flower with nectar and long filaments, fitted for sphingids (*Capparis*). Its stigma had to be brought into the outer, sexual plane. As the formation of a style seems to have encountered difficulties in this family with sessile commissural stigmas, the entire pistil was elevated by a gynophore. As demonstrated by Stebbins (1950, pp. 503–510) this single ecologism may have brought about reorganization by means of selection. The first change became a central family character. In more advanced types, like *Cadaba*, the stamens too were elevated and the petals turned upwards. The handicaps of the absence of a flower tube and the presence of basal nectar accessible to all insects were overcome by the development of long tubular nectaries. I believe that the stiped ovary in this group does not have a merely protective function (Grant, 1950a).

Good (p. 349, 552) found "senseless repetition" of this syndrome in *Isotoma* (Lobeliaceae), *Clerodendron* (Verbenaceae), *Saponaria*, *Silene*, *Phlox*. Of course the repetition is due to convergence.

Miscellaneous Pollination Classes

In phalenophily (pollination by small moths) the floral characters are like those in the preceding class but are less conspicuous in color and length.

With regard to psychophily (pollination by butterflies), plate II of Vogel (1954) shows the characters of this class. In his table of differential characteristics (p. 38–39) we find: (1) colors diverse, including, however, the scarlet of non-ornithophilous European flowers; (2) nectar-guide; (3) long narrow tube or spur with a flat wide margin; (4) margin not deeply dissected; (5) agreeable odor; (6) diurnal; (7) tender tissues.

Myrmecophily (pollination by ants), malacophily (by snails), and batrachophily (by frogs) are dubious classes, probably to be considered as outdated. I gave reasons for this in regard to ant pollination, considering the published cases as incidental (van der Pijl, 1955, p. 191). The batrachophily of the orchid *Lissochilus roseus* in Morocco sounds questionable (Guinea, 1946, read in abstract only). I have described cases where a frog (*Rhacophorus*) was regularly found on *Alocasia* inflorescences and a lizard (*Hemidactylis*) on *Artocarpus* inflorescences (van der Pijl, 1933, 1953). D'Ewes (1959) reported an "arum-frog" (*Hyperolius horstocki*) as a regular visitor to *Zantedeschia*. In all these cases the vertebrates were seeking insect visitors in the flowers.

Ornithophily (Pollination by Birds)

A long-lasting battle since the 1920's has led to the general recognition of ornithophily as a class (cf. Werth, 1915). The work of Porsch (1923, 1933, etc.) was largely responsible for this. Melin's book (1935) was a belated regression by a writing-desk critic with an interest in marginal, not harmonious relations. Vogel (1954), though anti-selectionistic himself, criticized Melin's negativism extensively. The interest in demarcation and classification shall here be replaced by more positive elements.

Ornithophily has originated independently on different, older, eco-morphological

substrata. So the class has differently constructed flowers, a situation which has been used by Melin and Werth, followed by Kugler, to belittle its existence as a class. It is rare in the lower families, though appearing in Capparidaceae, Cactaceae, Proteaceae, etc., but is widespread in tropical Leguminosae and Tubiflorae. We can follow its emergence in groups with recent speciation, whereas it is supraspecific in other groups.

The adaptations in the birds also arose parallel in many groups and in many ways, perhaps via simple quenching of thirst in arid zones, via destructive eating of flowers, or via the catching of insects, even through boring for insects in tissues accompanied by a flow of sap. As to the latter I refer to some woodpeckers like the Asiatic *Dryobates analis* (Spennemann, 1932; Cammerloher, 1928; Docters van Leeuwen, 1931). In regard to the catching of insects in flowers, it is necessary to remark that this is a rare exception, though the old stories about it are still repeated. Melin upholds (p. 104) the opinion, impossible to any real observer, that hummingbirds are not dependent on the nectar of flowers.

In a sense the flower birds have not become as narrow flower-animals as some bats (the Macroglossinae). The birds cover their needs of protein outside the flower. Data on pollen consumption are rare. Melin collected some old ones (pp. 76, 172, 196).

There exist, as already discussed, many transitional flower forms, interesting from an evolutionary viewpoint. Spennemann (1932) and others described cases where frugivorous birds are semidystrophic, plucking off flowerparts. In some instances unadapted birds are legitimate visitors and instrumental in pollination, when solid foodbodies are offered, whereas the sexual organs are protected. Porsch (1923) described how in *Freycinetia funicularis* edible bracts were eaten by bulbuls. The most curious one is the *Boerlagiodendron* (*Osmoxylon*) mentioned by Beccari (1877, p. 194), as attracting pigeons as pollinators by means of false fruits between the flowers. Lam (1945, p. 75) described the phases of false and true fruit-formation.

The old, often-repeated instance of edible petals in *Feijoa* (*Orthostemon*) has now to be discarded. Werth (1943a) reduced it to ordinary ornithophily with nectar. Schroeder (1947) even showed that it is a bee-flower. The still more famous case of *Marcgravia* is discussed below.

According to Melin a bird visits a certain flower "attracted" by some character which is present only incidentally. He cited many incidental visits to apparently non-adapted flowers—which seems not astonishing. Singh (1933) also recorded such visits as to the fragrant *Morinda tinctoria*, but was mistaken in thinking that scent might help; he also considered *Strelitzia* and other bird-flowers as not adapted for birds.

I might add many more instances like this, as of brooding sunbirds visiting flowers in the neighborhood which they otherwise neglect (van der Pijl, 1950, p. 147). Usually, however, the better adapted flowers are chosen by birds. In this context it should be related that though these birds show no flower constancy there is surely competition for birds between different flower species. Sometimes a much-visited species is left when another starts flowering. Docters van Leeuwen (1933, p. 102) described how a sunbird visited all kinds of flowers in the summit region of a volcano, in open competition with insects.

The excluding nature of some of the characters, giving the final touch to the syndrome, is especially clear in the oblique profile of some Cactaceae and in some Labiatae, which do away with their underlip in different ways. Docters van Leeuwen (1938) pointed to the shrivelled lip of *Leonotis*. I could demonstrate (1950, p. 150) how a bumblebee could, with some difficulty, still manage some intermediately ornithophilous *Salvia* spp., but not the well-adapted *S. splendens*.

The full syndrome of characters, as already stated by Porsch, Werth, and even by Delpino, is (in accordance with the physiology of birds): (1) diurnal anthesis; (2)

odorless; (3) visual flower with vivid colors, often scarlet or with contrasting parrot-colors; (4) honeyguide absent or simple; (5) rather deep nectar in large quantity; (6) reduction of corolla margin, leading to tubular corollas, even in Choripetalae; often brush type; (7) mechanical strengthening by fusion of flowerparts or by mechanical tissue; (8) often capillary systems for the nectar.

I could clearly demonstrate (1937b) a differential diagnostic character between American and Old-World bird flowers, already indicated before by Delpino (1875) and Porsch (1934) and others. In accordance with the different approach by their visitors (resp. hovering and sitting) there is a difference in position and perching possibility. The exceptional American plant with a perch (*Puya*) was again described by Gourlay (1952) as pollinated by exceptional birds. Vogel (1954, p. 44) denied this geographical difference, using my conclusion in the opposite sense. Disharmony of American plants in Java was answered by puncturing. Short-billed hummingbirds do so with more Andine bird-flowers.

Puncturing by birds is a dangerous side-effect of a labile interrelationship. Swynnerton (1915–1917) described it for plants in South Africa where sunbirds had no sufficient perch. There seems to be much puncturing by short-billed birds in the large-flowered *Sesbania grandiflora* (Tiwary, 1927). The general puncturing of *Hibiscus rosa-sinensis* (cf. Swynnerton, 1915–1917, and van der Pijl, 1937b) is mysterious if the plant is indigenous in the Old World. Werth relates in a chapter on ornithophily, full of long disproven conclusions, that a sunbird visited its flowers while hovering before them (1956, p. 132).

The dominance of scarlet flowers in ornithophiles and therefore in ornithophilous floras, has often been attacked as unreal. Melin did this, but his own table 1 A proves it statistically. Weevers (1951) thought he had disproven the phenomenon by statistical comparisons, but these seem too coarse, putting all shades of pink and red together and leaving out figures from Central America and the Andes. Pickins (1955) also gave a statistical elaboration on this point.

Good (p. 328) considered the queer color combination of yellow and red in many flowers as autonomous repetition. Needless to say, all his instances are bird-flowers, as is his pair *Antholyza-Leonotis* (p. 351).

When studying diversification in groups with growing ornithophilous tendencies, taxonomists should keep the co-adaptive syndrome in mind and not only consider the separate characters independently. Taxonomists analyzing the characters of a group statistically in the way recommended by Sporne and finding some correlation should not neglect the existence of such "adaptive peaks" of an ecological nature (cf. Stebbins, 1951).

We can follow the evolution of the syndrome in many families, as Porsch (1937) did for the Cactaceae. Ornithophily became dominant in the Andine genera, viz. in the suprageneric group of *Loxanthocerei*, where first a tube, later zygomorphy and reduction of ventral flower parts developed. Vogel pointed to the contrast of Cactaceae with the succulent Asclepiadaceae, where the pre-existing organization apparently did not lend itself to ornithophilous reconstruction. In the Andes even the Compositae have reached ornithophily in *Mutisia* spp. which hang down like a *Fuchsia*.

The long-tubed, red *Salvia splendens* with reduced lower lip from the Andes is a nice contrast with blue temperate Salvias (bumblebee flowers), making another sudden change in organization type. This is still more obvious in andine *Scutellaria* spp. There is not enough space here to follow the reorganizations in tubiform choripetalous Malvaceae, or the improvising of tubes from flowerparts in *Cuphea*, *Cadaba*, *Tropaeolum*, *Fuchsia*, etc.

Grant (1950a) made the suggestion that the strong staminal tube of Papilionaceae might be a protective relic-condition of a formerly more completely ornithophilous, tropical family. The symmetry pleads against birds. A decision is difficult as the

family is old and we do not know the time of appearance of regular flower-birds. I made parallel suggestions as to its tropical origin, based on extrafloral nectaries near the flowers (1954) and on the testa of its seeds (1956a).

It is known that in the Loranthaceae the tribe *Loranthoideae* is strongly ornithophilous. Docters van Leeuwen (1954) collected many data and personal observations from Java, also on the curious Dicaeid birds which show double adaptation to the plants, viz. as pollinators and as seed-dispersers with specialized stomachs.

Chiropterophily (Pollination by Bats)

There are old, incidental observations on bats as flower visitors. Firstly Burck (1892) in Java saw fruit-eating bats visit the inflorescence of *Freycinetia insignis*, well adapted to them, in contrast to ornithophilous sister species (confirmed by van der Pijl, 1956b). Hart (published by Knuth 1897) saw bats on the flowers of *Bauhinia megalandra* and *Eperua falcata* in Trinidad, Cleghorn (1922) on *Bassia latifolia* in India, Heide (1927) on *Markhamia stipulata* and *Kigelia* in Java, Danser (1929) on *Parkia* in Java.

Since 1922 Porsch has been the prophet of chiropterophily as a flower class; he predicted its characters, pointed to many possible instances and published the first purposefully investigated case (of *Crescentia*) in 1931. He compiled afterwards (1934, 1935, 1936) many data on the subject, adding deductions on such Cactaceae as *Carnegiea* (1939), later more or less confirmed by Allen's observations on some "Cereus" and by the finding of its pollen in the stomach of the bat *Leptonycteris nivalis*.

The present author published some preliminary notes followed in 1936 by an extensive monograph in German, adding and ascertaining many instances (species of *Agave*, *Musa*, *Adansonia*, *Ceiba*, *Durio*, *Sonneratia*, *Madhuca*, *Parmentiera*, *Oroxylum*, and *Gossampinus*. Later additions were *Mucuna* spp. (1941) and *Duabanga* and *Haplophragma* spp. (1956b).

Vogel (1954) added as a possible case for South Africa *Ipomoea albivenia* and later (1958) in a surprisingly rich paper on South America added species of *Enallagma*, *Trianaea*, *Drymonia*, *Campanea*, *Symbolanthus*, *Cobaea*, *Cayaponia*, *Cleome*, *Chelonanthus*, *Macrocarpaea*, and *Purpurella*. It is most interesting that the famous "ornithophilous" *Marcgravia* species here proved to be chiropterophilous. Some instances are based on deductions, others on direct observations.

Jaeger (1954) gave a review of the field in French and added further details on *Ceiba*, also on *Adansonia* in its natural habitat, Africa.

The characters of the main class, where pollen and nectar are eaten, are in accordance with the physiology of the bats in question. Bats are color-blind, have a good sense of vision and smell and a less well-developed sonar-system. The colors of the flowers deserve experimental research. According to Vogel (1958) they are functionless and just "Stil." He bases this on the same arguments Melin used against the colors of bird-flowers.

The syndrome is: (1) nocturnal anthesis; (2) whitish or drab colors, sometimes pink or dark-reddish; (3) large and strong flowers or inflorescences; (4) exceedingly large quantities of nectar, up to 15 cc; (5) unfresh smell, reminiscent of fermentation; (6) large quantities of pollen (large or many anthers); (7) a peculiar position outside the foliage, enabling bats to alight and depart easily.

The position of the flower often takes the form of cauliflory or flagelliflory (penduliflory), with the flowers dangling on long slack stalks. (A few ornithophiles also show some flagelliflory.) A pincushion-type, with projecting flower-stalks, also occurs. The "pagoda-tree" of Bombacaceae (cf. van der Pijl, 1957, p. 360) is also a favorable "bat structure."

The typical claw marks of the thumbnails on the flowers betray the nightly visits of bats.

The bats involved are all tropical though some migrate to the southern U.S.A.

In the Old World we meet with the Megachiroptera, known as fossils since the Eocene (Monte Bolca). The most primitive forms are the Pteropinae, true fruit-eaters. A more specialized group, the Macroglossinae, reduced in size, feeds on nectar and pollen only and has rudimentary teeth (except for the canines) and a very long tongue.

In the New World Megachiroptera belonging to the subfamily Glossophaginae evolved independently into fruit-eaters, and some more or less into nectar-eaters. This must have occurred more recently.

We may suppose that Pteropinae first acted on flowers as destructive eaters. An apparently recently immigrated *Pteropus* in Australia feeds on *Eucalyptus* flowers and already shows signs of degeneration of the teeth (Rathcliffe, 1931). In Java I found *Durio* flowers squashed by bats and this happens more in regions to the east (*Melaleuca*, *Eugenia*). Being also fond of bleeding sap (fermenting or not) *Pteropus* can incidentally lap up nectar, leaving the flowers intact and pollinating them, as reported by McCann (1931, 1934) for ornithophilous species of *Grevillea* and *Bombax*.

The smaller Asiatic fruit-bats of the genus *Cynopterus* behave in the same way but are more apt to become incidental pollinators (McCann, 1931, Hanelt, 1959). In Java they are sometimes semi-destructive on *Parkia* (van Heurn, 1929), but were never seen as real pollinators of normal bat-flowers. I never found pollen in the numerous intestines dissected. Only the Macroglossinae, eating pollen as a source of protein, are effective there, and bat-flowers often have a large quantity of pollen.

In Africa the macroglossine bat *Megaloglossus* seems to be rare, perhaps due to the lack of flowers throughout the year. Observers in Africa (Jaeger, 1954) found smaller Pteropinae on bat-flowers, one (*Eidolon*) even eating pollen. Baker and Harris (1957) reported them as the actual pollinators of *Parkia* and photographed them later also on *Kigelia* and *Ceiba*.

As the smell of typical bat-fruits and bat-flowers is the same and as Pteropinae only swallow the juice of fruits, the transition is easy and understandable. The smell, perhaps due to butyric acids, is not a signal as in bees, but acts directly on an innate sense (cf. the experiment in van der Pijl, 1936, p. 28). It seems related to the smells of bats themselves and has some stimulating effect.

In a small group of flowers, the subclass with solid food-bodies (containing *Bassia*, *Madhuca*, and *Freycinetia*), the fruit-bats remain the obligate pollinators (Cleghorn, 1922, van der Pijl, 1936, 1956b). It is uncertain whether the cases of *Pachira insignis* (Porsch, 1937) and *Eugenia cauliflora* (Porsch, 1941) can be included. The latter has the typically large anthers of the main class.

In the New World the differentiation of flower-bats seems more recent and less pronounced. The diets of the bats are often mixtures of insects, fruits, and nectar. It is, therefore, the more curious that the bat-flowers of the New World show the full type and fit perfectly to Asiatic Macroglossinae.

The relatively recent nature of chiropterophily is reflected in the distribution of bat-flowers among the plant families. The bat-flowers are loosely spread over many of the higher families, as changes from other classes. In the Ranales bat-fruits are known, but bat-flowers not. The complete list of known bat-flowers contains about 40 genera in 22 families, Monocotyledons and Dicotyledons from Capparidaceae and Cactaceae onwards. One can mention such families as the Bignoniaceae, Bombacaceae, Cactaceae, and Sapotaceae. Some cases stand more or less isolated (*Agave*, *Cobaea*, *Symbalanthus*, *Campanea*, *Freycinetia*, *Musa*, *Parkia*, etc.).

Vogel (1958) used this to fortify his anti-selectionistic concept, when discussing the remarkable case of *Purpurella* in the Melastomaceae, a family with pollen flowers. The case becomes less surprising when we see that flowers of sister species, though perhaps bumblebee flowers, secrete much nec-

tar, and that the related *Brachyotum* is ornithophilous.

In the Cactaceae (Porsch, 1939, p. 119–133) chiropterophily seems to have evolved in some separate species of *Cephalocereus* (*Pilocereus*), *Carnegiea*, *Pachycereus*, and *Lemaireocereus* on a common basis with sphingophily, together with cauliflory. Probably some species are transitional. Judging by the broad tube, the color, the nightly anthesis and the large anthers of the newly discovered *Cephalocereus machrisii* from Brazil I was able to predict to the discoverer (Dawson, 1957) that it would emit a sour smell at night. Later Dawson confirmed this.

The chiropterophilous *Cleome anomala* (Vogel, 1958) is also clearly derived from the sphingid flowers of other Capparidaceae.

In *Freycinetia* and other genera the basal type seems to be ornithophilous. This has also been presumed for *Musa*, but the true ornithophiles from the section (or genus) *Ensete* are subtropical and peripheral. In the remaining sections *Musa* proper apparently contains some ornithophilous species in addition to a majority of chiropterophiles. The oldest group (*Eumusa*) seems to be chiropterophilous. One of the ornithophilous *Musa* species (*M. sanguinea* Hook. f.) still gives off a chiropterophilous smell in the afternoon.

In the Bignoniaceae too sphingophily and ornithophily seem at first glance to be primary. On the other hand, there is in this old family chiropterophily in three different tribes, and some general tendency towards musty smells, which suggest old chiropterophily. *Spathodea campanulata* is certainly ornithophilous and of the Old World type with the sexual organs pointing toward the inner part of the inflorescence. It is, however, not fit for sunbirds, but attracts less specialized, larger birds (Cammerloher, 1928, van der Pijl, 1936, Ali, 1932, Docters, 1938). The whole plant and also the flowers possess the musty smell. The opinion of Vogel (1954, p. 256), that the smell (not conforming to the "Stil"!) is due to microbes in the nectar, is most improbable (cf. Winkler, 1907). The flowering plant has, moreover, the pincushion-form of *Markhamia* spp., whereas the flowers, though rimless, thin-walled, diurnal and fiery red, are wide-mouthed. This is transitional to the the closely related complex of *Markhamia-Haplophragma-Pajanelia*, with strong chiropterophily. Sprague (1919) split off from this complex (incl. *Spathodea*) the sphingophilous plants as *Dolichandrone*. A rare case of taxonomy on a flower-ecological basis!

In the Bombacaceae, we also find transitional types, in which the direction of the transition is not clear. *Bombax malabaricum* is certainly not specially nocturnal and is ornithophilous, though not conforming completely to the type, and it is popular with unspecialized birds such as starlings and crows (Spennemann, 1932). The large, open flowers, however, have the same musty smell as *B. valetonii*, a bat-flower. In Java I found no bat-visits, the bats preferring other trees in the neighborhood, but Hahnelt (1959) relates that the flowers are eaten by *Cynopterus* in southern China, and McCann (1934) saw *Pteropus* lapping nectar from them while still open at night.

The same transitional condition was reported by myself (1941) for the low climber *Macuna pruriens*. The flowers of the plant are dark-purple and smelly, but are ignored by bats and actually visited by birds (Docters, 1938). Many sister species—in the Old and New Worlds—are truly chiropterophilous, while others are beautifully ornithophilous (Docters, 1938).

In the Solanaceous tribe *Hyoscyaminae* there seems to be some pre-adaptation towards chiropterophily. The low Himalayan *Scopolia luridus* has clearly a part of the syndrome (pendulous, sour-smelling, lurid color, but probably not nocturnal). The American *Trianaea* spp. described as chiropterophilous by Vogel (1958) seem to be more related to the *Datureae*, in which on the other hand nocturnal anthesis of large hanging flowers is found as prerequisite. Some *Solandra* species may be, or may have been, chiropterophiles.

In the Sapotaceae (and perhaps *Musa*, *Sonneratia*, and *Parkia*) there is a pre-existing bat-smell which functions in seed-dispersal. Sometimes the smell is even emanated by the leaves (van der Pijl, 1936, p. 28). In the Bignoniaceae such relations are only possible in the *Crescentiae*. In the Bombacaceae such older relations are not probable, but Vogel (1958, p. 511) points to a pronounced bat-smell in the fruits of a *Drymonia* species (Gesneriaceae) whereas other species have bat-flowers.

(In my studies on seed-dispersal (1955a) I pointed out that there is a difference in phase between the dispersal of spores and of seeds by vertebrates. Though seeds are later developments than spores, the relations of herbivorous reptiles with seeds probably developed earlier than those of vertebrates (or even bees) with spores. Birds and mammals could easily take over dispersal when fruits had originated. Fruit-bats likewise existed before flower-bats, though flowers precede fruits historically and ontogenetically.)

Baker and Harris (1957) pointed to a discrepancy between three facts regarding the bat-pollinated genus *Parkia*. These are, (a) the pantropical distribution of *Parkia*, which can only have happened from America before the Eocene and via Beringia; (b) the absence of Megachiroptera in America; (c) the much later evolution of microchiropterous fruit-bats. This makes them suggest that the *Parkia*-type of inflorescence might be a fortuitous pre-adaptation. I agree that some basal requirements for parallel development may originally have been present, such as much nectar, large "flowers" with much pollen, nightly anthesis. I already pointed to a "pre-adapted" "bat structure" of the crown in chiropterochores (1957).

An analysis of the genus *Mucuna* with both American and Asiatic chiropterophiles might also be valuable. The most chiropterophilous families, the Bignoniaceae and the Bombacaceae evolved parallel genera in the Old and New World with bat-flowers. Most American cases of chiropterophily, however, have evolved de novo in world-wide families without parallels in the Old World, in the same way that *Salvia* species in the Old and the New World developed ornithophily independently.

Chiropterophily and chiropterochory have implications in synecology, physiognomic changes and geographical distribution. The author published (1957) a map of the distribution of Macroglossinae and Pteropinae in the Pacific area and found some bat-flowers or bat-fruits which have the same eastern limits as the bats. Nur (1958), confirming the chiropterophily of *Musa textilis*, brought the distribution of some sections of *Musa* into a map, together with the corresponding distribution of Macroglossine genera.

The author also pointed (1936, 1956b) to the synecological factor of common pollinators linking some chiropterophiles in a vegetation. A succession of flowering periods throughout the annual cycle make the life of both bats and plants possible. In single cultures of *Ceiba* only those trees near gardens with *Musa*, *Parkia*, etc., were visited. This interdependence deserves special research when but one chiropterophile is known from a region.

Chiropterophily (and chiropterochory) make clear why flagelliflory and cauliflory are confined to the tropics. There is no common taxonomical, morphological and anatomical basis for the cases of cauliflory. I gave in my articles (1936, 1941, 1956b) a review of all the old theories on this phenomenon, now almost entirely superfluous because the right ecological approach has been found. For the majority of cases, where the flower is not chiropterophilous, I found bonds with the dispersal of seeds by fruit-bats (van der Pijl, 1957). Fruit-bats have left an earlier but quite comparable stamp on many tropical fruits.

In the tropics many more mammals play a role in pollination than in temperate regions. Many squirrels there like nectar and are not as destructive as the temperate ones. The same is true of some insectivores and marsupials. Porsch (1934–1935) collected

many data on this point, so interesting for the Australian region.

At the end of this discussion of flower-classes from a dynamic angle it would be interesting to study the pollination-spectrum of some orders and families. There are old trials of this kind (Müller, 1873, p. 413). Porsch (1938–1939) made an attempt in this direction for the Cactaceae. Vogel (1954) did so for some genera and families in Africa. The Orchidaceae deserve such a special study. Vogel (1959) started it in a brilliant analysis of South African Ophrydeae. In the forthcoming Vol. II of his book on the Polemoniaceae, Grant promises a complete review of its pollination systems.

Up until now such classifications, as we saw, produced no grand reforms in taxonomy.

It might be interesting to study the relations between flowers and changes in climate and the importance of flower-ecological spectra for synecology, plant-formations, and local floras. Docters van Leeuwen (1933) gave a fine survey for a tropical mountain-region.

It is in agreement with our views that the direct influence of the climate on flowers is unimportant and more or less limited to anemophily and rain-pollination (Hagerup, 1951). Notwithstanding the opinions cited by Jaeger (1957, p. 308) the geographical variations in flower-characters seem to be influenced via the changes in pollinators (cf. also Weevers, 1951).

As a student of plant-dispersal I am also tempted to compare our finds with the evolution of fruits, which offers a parallel development of primitive and progressive classes, both crossed and influenced by the dispersing agents (cf. van der Pijl, 1956).

Admitting the heavy burden already placed on modern taxonomists, one should nevertheless state that flower-ecology (and seed-ecology) are important to them. The two fields do not deserve the neglect shown by the four pages out of 407 in Richards' "The Tropical Rainforest," nor the total omission of pollination in the chapter "Factors of Distribution" in Good's "Geography of Flowering Plants."

Summary

1. The study of flower-classes does not lead to delimitations of groups, but can supply the ecological background for evolutionary trends in such groups. The preference of visitors is not, as thought by Goebel, always just utilization of a loose incidental character.

2. In the class of sapromyophiles a complex of characters fitted for flies is demonstrated to be a convergence. This explains much in the Annonaceae. In some orchids regression to fly pollination leads to a return to radial symmetry. Knowledge of the character complex serves to revise the separation of genera for conspicuous structures, still inside the ecological complex (*Cryptophoranthus* and *Cirropetalum*).

3. In one of the melittophilous subclasses, viz. the *Xylocopa*-flowers, there evolved a new protection against "unwanted" activities of rude pollinators, an ant-guard. The failing of such contraptions in flowers for birds and bumblebees, used by anti-selectionists, seems an as yet unbalanced condition.

4. The study of the floral spectrum of some families has divulged that some "ecologisms" have already become suprageneric "morphologisms." The parallelism of forms in distant groups is not undirected, kaleidoscopic morphological repetition as believed by Good, but is convergence.

5. In ornithophiles we also find a typical complex of characteristics though superimposed on different, older, "morphological" substrata. There are many transitional flowers, fitted for unspecialized birds. Independent development in the Old and New Worlds has led to differences in style.

6. In chiropterophily we find transitional cases, visited by transitional nectar-bats, still mainly destructive. Some families, as Bignoniaceae and Cactaceae, show a preadaptive basis, sometimes leading separately to bat-pollination in Old- and New-World forms. Some points of the syndrome

(flagelliflory and cauliflory) explain typically "tropical" characteristics. Seed-dispersal by bats may also provide a pre-adaptive basis.

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CHANGES IN THE VARIATION PATTERN OF A HYBRID POPULATION OF *HELIANTHUS* OVER AN EIGHT-YEAR PERIOD[1]

G. L. Stebbins and K. Daly[2]

University of California, Davis, and Brookhaven National Laboratory, Upton, New York

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Introduction

Recent studies of natural populations of higher plants have pointed consistently to the hypothesis that hybridization between populations having markedly different adaptive properties, particularly if it occurs in a disturbed, changing environment where new ecological niches are likely to be available, is one of the strongest factors bringing about evolutionary change (Stebbins, 1959). Consequently studies of such populations, even if carried out over the relatively short periods of time available to the average investigator, should yield valuable information about the evolution of natural populations. The annual species of *Helianthus*, or sunflowers, are particularly favorable for this purpose. They are variable, widespread, and weedy, entering often into disturbed habitats. They are cross-fertilizing, due to self-incompatibility. Hybridization between species occurs frequently, and the interspecific hybrids, although highly sterile, nevertheless can produce some offspring, particularly through backcrossing, or introgression. There is some evidence that the variation of some species has been increased by this process. Since all of the annual species have the same chromosome number, n=17, evolution within the group has not involved polyploidy. Finally, the group has been subjected to a series of careful cytotaxonomic studies by Heiser (1947, 1949, 1951a,b, 1954) from whose work the above information was obtained.

The two annual sunflowers of California, *Helianthus annuus* and *H. Bolanderi*, occupy different ecological niches. The former is a weed of roadsides, very common in the Central Valley and in Southern California. The commonest subspecies is subsp. *lenticularis* (Dougl.) Ckll., which was already in the state when the first botanical collections were made, and was used by the Indians for various purposes (Heiser, 1949). Since it does not now occur in natural sites in California, it was very likely introduced originally by the Indians from farther east. Since the advent of the white man, repeated introductions from the eastern states have almost certainly been made. The cultivated sunflower, *H. annuus* subsp. *macrocarpus*, frequently escapes to roadsides, and hybrids between the two subspecies are not uncommon (Heiser, 1949, 1954). *Helianthus Bolanderi*, on the other hand, is a native, endemic species, its natural range extending from southern Oregon to south central California. It consists of two races, one of which is found in the inner coast ranges and Sierra foothills, chiefly on serpentine soil; the other is a ruderal plant which replaces or occurs with *H. annuus* subsp. *lenticularis*, in the western part of the Sacramento Valley, particularly in Solano, Yolo, and Colusa counties. Heiser (1949) made artificial hybrids between *H. annuus* and *H. Bolanderi*, and compared them directly with the natural hybrid swarms. He found that the F_1 hybrids had variable pollen and seed fertility, ranging mostly between 2 and 10 per cent. Meiosis in them is somewhat irregular, with chains of 6 chromosomes being usually found and chains of 8 occasionally. The two species differ, therefore, by several reciprocal translocations. Plants of backcross progenies have fertility values ranging from as low as the F_1 hybrids to as high as the parental species.

[1] Part of this study was carried out at Brookhaven National Laboratory under the auspices of the U. S. Atomic Energy Commission.

[2] Present address: Department of Biological Sciences, San Fernando Valley State College, Northridge, California.

Location and History of the Population

The hybrid swarm which is the subject of the present study is located 5.4 miles east of Davis, Yolo County, California. It was first found by Heiser in 1946 and described by him under the collection number *1859*. At the time, it consisted of a few hundred individuals, among which were hybrid progeny of at least the F_2 generation. Since the four-lane, divided highway along which it is located was finished in 1941, the establishment of the parental species in the locality is unlikely before that date. Consequently, the F_1 plants which gave rise to the hybrid swarm probably appeared first not earlier than 1942 or later than 1945. Since that time, repeated hybridization between *H. annuus* and *H. Bolanderi* has undoubtedly occurred in the locality. Hence, the population of 1951, the first studied by the present authors, probably contained progeny of every generation from F_1 to at least F_7, but not beyond F_{10}.

The population itself occurs in a depression bounded on the north by tracks of the Southern Pacific Railroad and on the south by U. S. Highway No. 40. The area is about 700 meters long from east to west, and 16 meters wide. The underlying soil is a clay loam of alluvial origin. The associated vegetations are entirely herbaceous and ruderal, consisting principally of the following species, in approximate order of abundance. Identifications are according to Munz and Keck (1959).

Perennials:

Distichlis spicata (L.) Greene var. *stricta* (Torr.) Beetle
Sida hederacea (Dougl.) Torr.
Rumex crispus L.
Lippia nodiflora Michx. var. *rosea* (D. Don) Munz
Grindelia camporum Greene
Heleocharis palustris (L.) R. & S.
Ambrosia psilostachya DC.
Alisma triviale Pursh
Machaerocarpus californicus (Torr.) Small

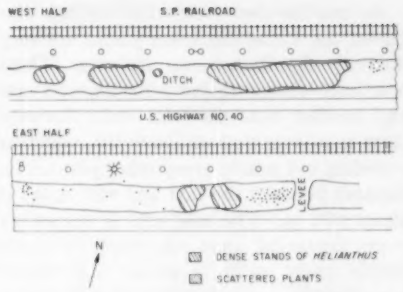


Fig. 1. Diagram showing the locality east of Davis where the hybrid swarm occurs and the distribution of *Helianthus* plants in 1951. The circles between the railroad and the population represent telephone poles which are about 40 m apart and were used as landmarks.

Annuals:

Polypogon monspeliensis (L.) Desf.
Xanthium strumarium L. var. *canadense* (Mill.) T. & G.
Melilotus indicus (L.) All.
Atriplex patula L. subsp. *spicata* (Wats.) Hall & Clem.
Lactuca Serriola L.
Centaurea solstitialis L.
Eryngium Vaseyi Coult. & Rose var. *vallicola* (Jeps.) Munz
Crypsis niliacea Fig. & DeNot.
Holocarpha macradenia (DC.) Greene
Aster exilis Ell.
Lythrum tribracteatum Salzm. ex Ten.
Polygonum aviculare L.
Erodium cicutarium (L.) L'Hér.
E. moschatum (L.) L'Hér.
E. Botrys (Cav.) Bertol.

The presence of several species characteristic of wet places reflects the fact that in normal years the area is covered with standing water for 2–3 months during the winter. Germination of *Helianthus* seeds usually takes place in April or May, as the water dries up, but complete absence of rainfall after April or early May, combined with high temperatures and low atmospheric humidity during the summer, makes the soil cracked and dry for some distance below the surface in July and August, when the plants of *Helianthus* reach maturity and begin to flower.

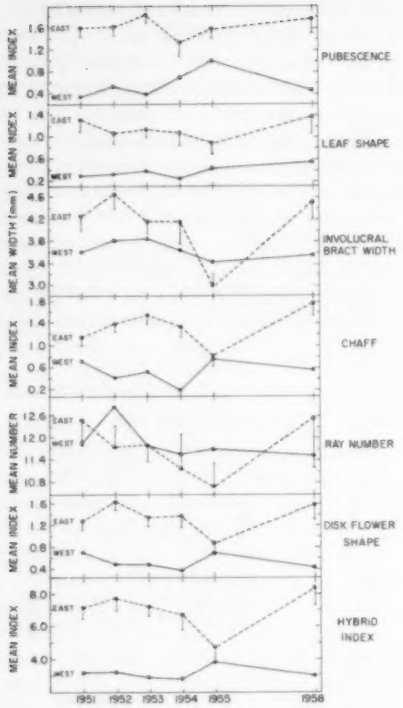


FIG. 2. Changes in six morphological characters and hybrid index in a hybrid *Helianthus* population during an eight-year period (range$=2s_{\bar{d}}$).

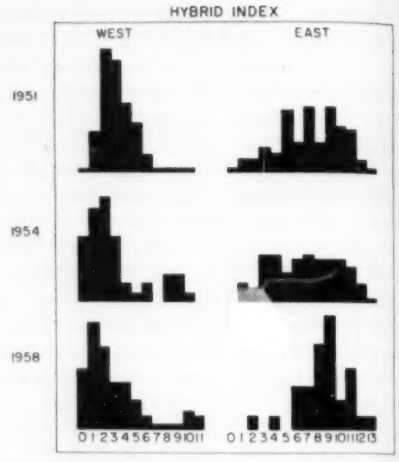


FIG. 3. Histogram of the hybrid index frequencies, expressed as per cent, in a hybrid *Helianthus* population for the years, 1951, 1954, and 1958.

toward *H. annuus*, one of these being disk flower shape in the east half. The remaining eight comparisons were found to be non-significant when tested.

The second question applied to the changing phenotypic discontinuity between areas over the eight-year period. With the exception of ray number, all other characters had shown significant differences in the analysis of variance (table 2) between eastern and western portions of the population. Hence, a test was made to determine whether the phenotypic gap between these two areas was greater in 1958 than in 1951. This difference, shown by (c) in table 1, was found to be significant for two out of six traits. For chaff and disk flower shape, east and west halves had become significantly less alike than in 1951. No case was discovered in which the two areas were now more similar than previously.

Groups of characters. Although the hy-

TABLE 2. *Analysis of variance of six morphological characters and hybrid index in a hybrid* Helianthus *population during the period, 1951–1958*

Source of variation	D. F.	Mean square						
		Pubescence	Leaf shape	Involucral bract width	Chaff	Ray number	Disk flower shape	Hybrid index
Years	5	1.49**	1.50*	26.15**	3.07**	41.35**	2.06**	38.76**
Areas	1	266.62**	142.73**	53.34**	154.04**	4.54	160.95**	9071.48**
Years × Areas	5	11.28**	1.86**	12.12**	9.75**	23.78**	7.30**	112.96**
Error	1120	0.36	0.51	0.87	0.36	5.62	0.43	6.41

* Significant at 5% level.
** Significant at 1% level.

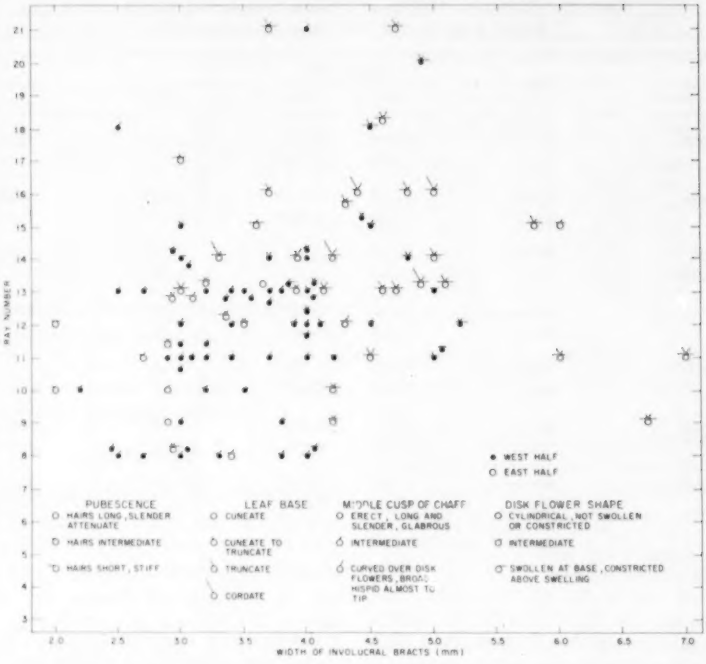
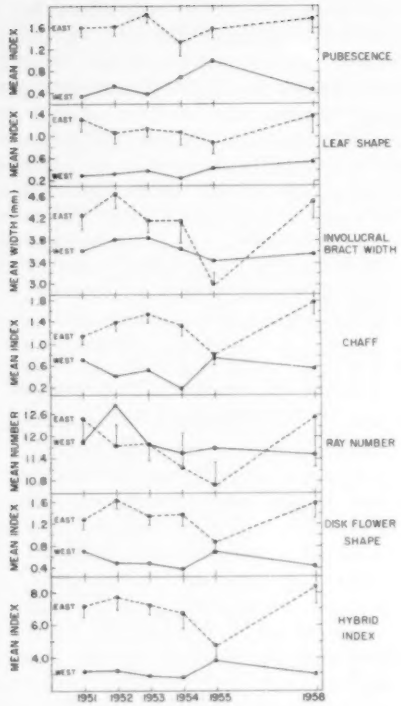


FIG. 4. Pictorialized scatter diagram representing the variation in six morphological characters in the 1951 population.

brid index may range in value from 0 to 17, the maximum value found in any of these samples was 14. The frequency distributions for hybrid index values shown in figure 3 reflect this fact, since they are all shifted toward *H. Bolanderi*.

When the variation in hybrid index was tested in the analysis of variance (table 2), highly significant differences were found in both years and areas. Comparison of the mean values for hybrid index in 1951 and 1958 (table 1) showed that in the western portion of the population no real net change had occurred, but that the east half had shifted significantly in the direction of *H. annuus*. However, the significant shift toward *H. annuus* in the east half is a reversal of the trend which developed in the previous years. During the period of 1952 through 1955, the east half showed a significant trend, not toward *H. annuus*, but in the direction of *H. Bolanderi*. The change in the east half alone between 1955 and 1958 accounts for the fact that in 1958 the east and west halves were significantly farther apart phenotypically than at any previous time during the study.

As a method of measuring character association, pictorialized scatter diagrams were prepared for the 1951 and 1952 collections. Presentation of the data from a sample of the 1951 collection is found in figure 4. Inspection of the scatter diagram failed to show a strong correlation among the various characters. This is due in great part to the weak correlation existing between ray number and involucral bract width, which served as coordinates of the diagram. Individuals which have large numbers of ray flowers as well as wider involucral bracts, and thereby fall in the upper right portion of the diagram, tend to have a higher fre-



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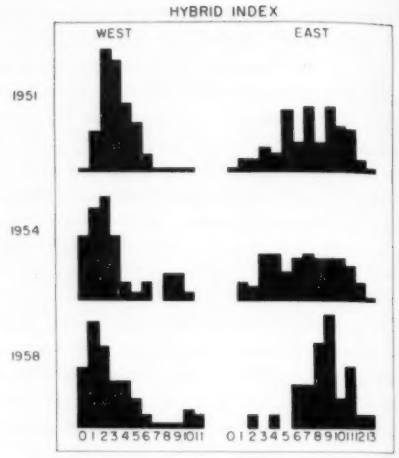

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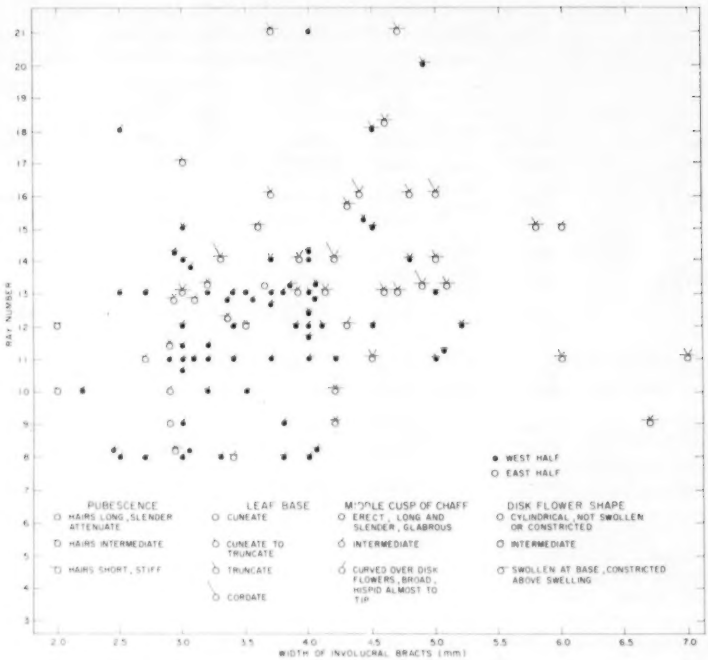

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TABLE 3. *Estimates of variances of six morphological characters and hybrid index in a hybrid* Helianthus *population*

Character	Area	Variance (s^2) 1951	Variance (s^2) 1958	Variance ratio (F)	Net change
Pubescence	West	0.253	0.513	2.02**	more variable
	East	0.355	0.323	1.10	–
Leaf Shape	West	0.286	0.426	1.49*	more variable
	East	0.995	0.516	1.93*	less variable
Involucral Bract Width	West	0.536	0.747	1.39*	more variable
	East	1.097	1.060	1.03	–
Chaff	West	0.205	0.482	2.35**	more variable
	East	0.308	0.185	1.66	–
Ray Number	West	6.509	5.180	1.26	–
	East	7.433	10.947	1.47	–
Disk Flower Shape	West	0.279	0.480	1.72**	more variable
	East	0.550	0.254	2.16*	less variable
Hybrid Index	West	2.648	8.115	3.06**	more variable
	East	9.111	5.292	1.72	–

* Significant at 10% level.
** Significant at 2% level.

quency of rays on the symbols than those individuals which show smaller numbers of ray flowers and narrower involucral bracts, falling in the lower left corner of the diagram. Hence, there is evidence indicating that individuals which closely resemble either of the parental species in both these characters are more likely to resemble them in the remaining four characters. However, the numerous exceptions which are evident demonstrate that the character association in the population is not as strong as might be expected.

Variability. In addition to testing mean differences, comparisons were also made of changes in the variability of each character. To determine the effect of factors acting upon the population on phenotypic variability, changes in variance between 1951 and 1958 were tested using the variance ratio (table 3). In the west half, five out of six characters were found to be significantly more variable. Two characters in the east half, leaf shape and disk flower shape, were significantly less variable at the end of the eight-year period. The remaining five comparisons were non-significant. The hybrid index, which exhibited greater variability in the west half in 1958 than in 1951, showed no real change in the eastern portion of the population.

Pollen fertility. In 1949, Heiser described the relationship between fertility and morphology, based upon pollen samples from fifty-two plants from his 1946 collection (*Heiser no. 1859.*) He concluded that parental types showed higher percentages of pollen fertility than hybrid types. Although some obvious exceptions were noted, plants with lowest and highest hybrid index values had higher percentages of good pollen (table 4). Plants of intermediate index values, e.g., 7 and 8, tended to have low percentages of good pollen.

In the present study, determinations of pollen fertility were made from samples of both the 1951 and 1955 collections. When these are summarized according to their hybrid index (table 4), the parental types are still found to have higher percentages of fertility than those with intermediate index values, but the percentage of highly

TABLE 4. *Summary of samples of 1946 and 1955 collections scored for both hybrid index and pollen fertility (data for 1946 from Heiser, 1949)*

Pollen fertility	Hybrid index					
	1–4		5–8		9–13	
	1946	1955	1946	1955	1946	1955
80–100%	9	39	1	15	9	7
40–80%	2	9	1	7	2	3
0–40%	13	12	13	8	2	0

TABLE 5. *Population size and precipitation data for the* Helianthus annuus × Bolanderi *hybrid swarm east of Davis, Calif., 1950–1958*

Year	Numbers of plants		Total	Precipitation (mm)	
	West half	East half		Total	March–May
1951	10,000	1,750	11,750	409	51
1952	1,350	4,500	4,650	517	109
1953	11,150	10,550	21,700	418	112
1954	1,110	5,300	6,410	338	109
1955	8,800	8,200	17,000	352	80
1956	5,550	2,910	8,460	635	53
1958	73,700	1,150	74,850	719	234

fertile genotypes among plants having intermediate phenotypes has risen significantly during the 9-year interval from 1946 to 1955. The probable significance of this increase will be discussed below.

DISCUSSION

The principal interest of this study is that it records the persistence of a hybrid swarm for more than 13 generations, and that during this time significant changes have taken place in the genetic composition of the swarm. In interpreting the results, we ask ourselves three questions: first, to what extent have the recorded changes been influenced by natural selection; second, how has the barrier of reproductive isolation which existed between the parental species affected the behavior of the population, and third, what has been and what eventually will be the fate of this barrier as a result of persistent cross-pollination between the two parental species?

With reference to the action of natural selection, the first facts which must be considered concern the size of the population. As can be seen from table 5, the fluctuation in size was enormous, from a minimum of about 4,850 plants in 1952 to a maximum of about 74,850 in 1958. At no time, however, were the numbers small enough so that genetic drift could be expected to have significant influence in fixing or eliminating genes. On the other hand, even the greatest year-to-year increase was far below that which would have been expected if every seed produced in one year gave rise to an adult plant in the next year. Hence, selective elimination of seedlings might be expected to have occurred every year, and in some years this must have been very extensive.

The fluctuations in population size reflect in part the marked oscillations in both the total amount and the distribution of precipitation which are characteristic of the Sacramento Valley. To table 5 have been added figures for total seasonal precipitation, plus the amount which fell during March, April, and May, the months when *Helianthus* seedlings might be expected to begin growth, for each of the winters prior to the summer in which the recorded population counts were obtained. These data were kindly supplied by the Department of Agricultural Engineering, University of California, Davis. They show that the two maximal sizes, those of 1953 and 1958, coincide with years of maximal spring precipitation, while the small populations of 1954 and 1956 coincide respectively with a low total seasonal and a low amount of spring precipitation. On the other hand, the sharp drop in the population from 1951 to 1952, which occurred only in its west half, cannot be accounted for by the precipitation data. Data on population size for 1959 were not obtained, but it should be noted that the season 1958–1959 had the lowest precipitation of all (seasonal 277 mm, spring 15 mm), which resulted in almost complete absence of *Helianthus* from the west half area and a population of not more than a few hundred individuals in the east half.

A second factor influencing the *Helianthus* population is the change in the accom-

panying vegetation. This has been displayed most conspicuously in the spread of the perennial rhizomatous grass, *Distichlis spicata* var. *stricta*, which now forms solid mats in many of the drier parts of the site. Photographs taken by Dr. Heiser in 1946 indicate that little or no *Distichlis* was present at that time, and that the bulk of the original population occupied the area between the present east and west halves of the present population. Since this intervening area is now an almost solid stand of *Distichlis*, the separation of the originally continuous population into its two halves may well have resulted from the progressive invasion of this grass. Although scattered plants of *Helianthus* will in favorable years push their way through it, the presence of *Distichlis* effectively prevents the development of good stands of sunflowers.

The problem of the extent and manner in which these external factors have affected the genetic composition of the population is much more difficult to solve. Before it can be discussed, the nature of the changes which took place must be reviewed. From figures 2 and 3, four facts are evident. In the first place, the east and west halves of the population behave as if they were separate populations. Their hybrid index values were at all times significantly different from each other, and both these values and the mean values for the individual characters changed to different degrees and in different directions. Second, in every characteristic the values for the 1958 population showed a reversal of the trend which prevailed from 1951 through 1955. Third, the west half population varied much more from season to season than the east half. Finally, variation in the six characters mentioned was to some extent independent. Involucral bract width and ray number showed parallel variations, and to a lesser extent also the shape of the chaff and of the ray flowers. These two pairs of floral characters showed less similar variational trends, and the two vegetative characters, pubescence and leaf shape, were entirely different from them and from each other.

There is good reason for believing that the different behavior of the west and east half populations was due to different selection pressures rather than the effects of isolation *per se*. They are descended from the original population, and the distance between them, less than 150 meters, can be traversed in a few seconds by the bees which pollinate sunflowers. Transport of seeds from one half to the other is also a likely possibility. Hence the isolation between the two halves is far from complete. The lowering of the hybrid index of the east half between 1951 and 1955 was due chiefly to a marked increase in *Bolanderi*-like plants. This was particularly noticeable in the field. Since no other population of *Bolanderi* occurs within 3 miles of the locality, this increase must represent migration from the west half. These *Bolanderi*-like plants occupied somewhat drier sites along the margin of the colony. Between 1955 and 1958, these sites in the east half area were invaded by *Distichlis* and *Lippia*, which reduced the population of *Helianthus*, and left in 1958 chiefly the plants in the middle of the depression. The poor drainage and long period of standing water in this depression apparently favors plants which are intermediate in phenotype but vary more in the direction of *H. annuus* than *H. Bolanderi*. The fluctuation in the hybrid index of the east half is, therefore, best explained by assuming that introgression of genes from *H. annuus* into *H. Bolanderi* between 1946 and 1951 produced in the west half a variable, highly adapted *Bolanderi*-like population which invaded the east half area in 1954 and 1955, after which it became reduced in this area by competition with *Distichlis* and other perennial plants. Meanwhile that part of the east half population which persisted in its central depression changed much less, but during the whole period altered its whole character significantly in the direction of *H. annuus*. During this same period, the west half population retained continuously a small percentage of individuals with *annuus*-like and intermediate phenotypes, but the predom-

inant facies of the population remained that of *H. Bolanderi*. This was presumably due to the fact that environmental conditions in the west half area have been consistently most favorable to genotypes which are predominantly *H. Bolanderi*.

Our data suggest that in a heterogeneous habitat such as the one under discussion, the genotypic composition of populations of cross-fertilizing annual species of flowering plants is much more likely to be determined by natural selection than by either drift or gene flow. The population sizes recorded here, although much too large to permit drift or random fixation to alter their genetic composition appreciably in the period since its origin, are nevertheless small compared to most of the populations of annual plant species in California. They are minute compared to those recorded by Epling and Dobzhansky (1942), for *Linanthus Parryae*. On the other hand, the spatial isolation between the two halves of the population is minimal, and heterogeneity existed even between different sites of the east half population. Thoday (1959; Thoday and Boam, 1959) has shown that in artificial populations disruptive artificial selection can cause subpopulations to diverge even though a maximum amount of gene flow is maintained between them. Our results would suggest that given a heterogeneous habitat, disruptive natural selection can similarly overcome the largest amount of gene flow which one might expect to find between two adjacent but ecologically different niches.

In respect to the reproductive isolating mechanisms which originally separated *H. annuus* from *H. Bolanderi*, the most interesting result of this study is first that individuals with intermediate phenotypes have persisted in the population for seven to ten generations, and in the east half have actually comprised the majority of the population throughout this time. In this respect also, a remarkable difference can be noted between the two halves of the population. While in the west half the relatively small number of plants with the morphological characters of *H. annuus* have remained recognizably distinct from *H. Bolanderi* throughout the period of observation, so that the impression was given every year of two species coexisting and forming a smaller number of intermediate hybrids, the east half population has appeared more like a continuous spectrum of intermediate types. Plants resembling *H. annuus* as well as those corresponding to *H. Bolanderi* have appeared every year, but they have always been outnumbered by plants with an intermediate phenotype. The most plausible explanation of this difference is that the microhabitat prevalent in the east half area favors the intermediate individuals. The explanation of why these intermediate types have been able to persist is revealed by the changes in pollen fertility which have taken place. Although the original F_1 hybrids, judging from their counterparts which were produced artificially, probably had only 10 per cent or less of good pollen, even by 1946 the majority of plants with intermediate phenotypes had higher percentages of normal pollen than this (Heiser, 1949, fig. F). By 1955 the majority of these intermediate individuals had pollen fertilities of over 80 per cent, which approaches that typical of the parental species. Apparently the same phenomenon took place here which was observed by Müntzing (1930) in *Galeopsis tetrahit* × *bifida*, by Smith and Daly (1959) in *Nicotiana langsdorffii* × *N. sanderae*, and was inferred by Lewis and Epling (1959) on the basis of experimental evidence to have taken place in the origin of diploid *Delphinium gypsophilum*. Independent segregation of the genes responsible for the morphological differences between *H. annuus* and *H. Bolanderi* and of the chromosomal differences responsible for the sterility of the F_1 hybrid made possible the appearance of genotypes containing combinations of alleles derived from the two parental species but homozygous for either the original or new combinations of chromosomal segments.

Since plants with intermediate phenotypes have not yet been hybridized with either typical *H. Bolanderi* or *H. annuus*,

the chromosomal constitution of these intermediates is not known. Nevertheless, they set large amounts of seed, and the persistence of intermediate phenotypes as the predominant components of the east half population suggests that they are segregating less in the direction of the parental types than did the original hybrids, and could give rise to a true breeding intermediate population. In this respect they are behaving much like another hybrid swarm, in the genus *Amaranthus*, which occurs in the Sacramento Delta area about forty miles south of the present area (Tucker and Sauer, 1958). In *Galeopsis*, *Nicotiana*, *Delphinium*, and *Amaranthus*, the fact that the parental species are self-compatible (at least one of the parental species is self-compatible) suggests that the stabilization of the intermediate phenotypes was made possible by their ability for self-pollination. In *Helianthus*, on the other hand, both of the parental species are self-incompatible and partial stabilization of the intermediate type has occurred in spite of persistent cross-fertilization. This shows that given a sufficiently large population, with rather strong selective pressure in favor of intermediates, a well-developed barrier of chromosomal sterility can be overcome by segregation and selection acting together in a cross-fertilizing Mendelian population.

The persistence of intermediate types for about 8 to 10 generations suggests, that unless the population becomes wiped out by further habitat disturbance or competition with other species, the intermediates will remain in the population indefinitely. Although their chromosomal constitution has not been determined, the most likely situation is that a variety of structural homozygotes has been formed, which represent both parental types plus a series of intermediate recombination types. Assuming a minimum number of three independent translocations separating *H. annuus* from *H. Bolanderi*, which is a likely interpretation of Heiser's cytological data, we can designate the parental types respectively AABBCCDDEEFF and $A_bA_bB_aB_aC_dC_dD_cD_cE_fE_fF_eF_e$, where A_b and B_a represent chromosomes derived by reciprocal translocation between A and B, while C_d, D_c, E_f, and F_e are corresponding translocation products involving chromosomes C, D, E, and F. These could give rise to six homozygous recombination types: AABB-$CCDDE_fE_fF_eF_e$, $AABBC_dC_dD_cD_cEEFF$, $A_bA_bB_aB_aCCDDEEFF$, $AABBC_dC_dD_cD_c$-$E_fE_fF_eF_e$, $A_bA_bB_aB_aCCDDE_fE_fF_eF_e$, and $A_bA_bB_aB_aC_dC_dD_cD_cEEFF$. If all of these homozygotes plus the semisterile single heterozygotes should persist in the population, gene exchange would still be possible, and modifying genes could arise which would make the translocation configurations become more regularly oriented on the meiotic spindle, and thus increase the fertility of the heterozygotes. If, therefore, a hybrid swarm like the present one should persist for a long time in a habitat favorable to intermediates, the original barrier of hybrid sterility could become broken up into its genetic elements, and reduced to a series of structural differences "floating" in the population, such as is well known to exist in many plant species (Stebbins, 1950, chap. 12). It is not unlikely that some of these situations in natural populations have originated from hybrid swarms in the manner just postulated.

Summary

A hybrid swarm resulting from repeated natural hybridization between the annual, cross-fertilizing species *Helianthus annuus* and *H. Bolanderi* in a locality east of Davis, California, has been followed over an eight-year period. During this time, population size has fluctuated widely, due in part to different climatic conditions which have prevailed from one season to another, and in part to changes in the composition of the associated species, particularly the sod grass *Distichlis spicata* var. *stricta*. Invasion of this grass just prior to the beginning of the observations recorded here had divided the original population into two halves. These halves, although separated by a distance of only about 120 m, nevertheless behaved like separate populations. The west

half maintained continuously a high frequency of *Bolanderi*-like plants, as judged by Anderson's hybrid index method, but contained at all times some plants more or less typical of *H. annuus* plus a still smaller number of intermediates. The east half, which at the beginning of the observations had a modal frequency of intermediate plants, first changed in the direction of *H. Bolanderi* through the increase of *Bolanderi*-like plants in certain parts of the population, but between 1955 and 1958 reversed this direction due to elimination of these types, so that the net change from 1951 to 1958 was significantly in the direction of *H. annuus*. Between 1946, when the population was first sampled by C. B. Heiser, Jr., and 1958, the pollen fertility of plants with intermediate frequency increased significantly. The significance of these data are discussed in relation to the effects of natural selection in a heterogeneous habitat, and the effects of persistent hybridization on incompletely developed barriers of chromosomal hybrid sterility.

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MIMICRY IN PROCRYPTICALLY COLORED SNAKES OF THE GENUS *DASYPELTIS*[1]

CARL GANS

Department of Biology, The University of Buffalo, Buffalo 14, N. Y.

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An extensive and varied literature refers to various aspects of the coloration of snakes (cf. Cott, 1940; van Harnack, 1953; Mertens, 1946, 1956; Camin and Ehrlich, 1958), yet selective forces acting on the color pattern are poorly understood. Lack of information on predator pressures has led herpetologists to express widely differing opinions on the phenomenon of mimicry, the reality of which has long been accepted in other animals (cf. Darlington, 1938; Brown, 1953; Brower, 1958). Recently Dunn's (1954) paper on coral snake mimics elicited discussions by Brattstrom (1955), Hecht and Marien (1956), Mertens (1956), and Schmidt and Inger (1957).

Coral snakes and their mimics are brightly colored, marked with sharply defined rings of red, yellow, and black. Is such "startling" coloration essential to the existence of a model-mimic cycle, i.e., may a snake combine a procryptic and a warning color and thus serve as a model? Because aposematic colors in snakes are often emphasized by warning or display movements (Mertens, 1946), model-mimic situations may occur whenever several cryptically colored species share such a behavior pattern.

Recent studies of the African egg-eating snakes (Gans and Richmond, 1957; Gans, 1959) show that these snakes offer a test case. *Dasypeltis* not only has a similar warning behavior, but also a notable resemblance in color pattern to certain procryptically colored viperid species. The present state of our knowledge permits no definite conclusions, but our information is sufficient for a tentative analysis.

This analysis is offered because any case of presumptive mimicry should be discussed, and furthermore this discussion may focus attention on the subject. Only detailed observations, combined with field experiments, can lift this matter from the realm of mere speculation to that of fact.

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THE PROBLEM IN *DASYPELTIS*

The snakes of the genus *Dasypeltis* are unique among the Ophidia in being almost completely defenseless. They lack both an effective biting apparatus and the muscular development for constriction. Nevertheless they eat the eggs of birds that have both the size and the disposition to defend their eggs effectively. Most of these birds can inflict severe damage upon, if not kill, the defenseless predator. (Guthrie, 1932, mentions several reports of snakes devoured by robins and other birds.)

The scanty evidence suggests that *Dasypeltis* shows local or regional food preferences, preying upon both arboreal and ground-nesting species. Nests such as those of the (colonial) weaver birds, ground-nesting larks, and long-tailed widow birds, are placed in fairly exposed places. The snake

[1] Cost of illustrations partially defrayed by author.

must cross an unsheltered zone when climbing the tree or approaching the nest on the ground, thus further accentuating its problem. There are, of course, other oophagous snakes, but these are not obligate,[2] and the anatomical structure necessary for swallowing a hard-shelled, ovoid object assures that an unspecialized snake will be large enough to devour the adult birds as well. On the other hand, the specializations that permit the adult *Dasypeltis* to feed on eggs, large in comparison to its own size, bring this snake into contact with relatively large birds. It thus encounters an unusual hazard, in addition to the predators that prey on all snakes.

An examination of specimens and a study of the literature indicate that *Dasypeltis* reflects this situation in three ways: (1) the coloration is procryptic (i.e., showing color resemblance, obliterative shading, and disruptive coloration; cf. Cott, 1940) and adaptively modified in each of the habitats of the several forms; (2) all species (as far as known) possess a warning reaction; and (3) some evidence shows that at least one of the species (*D. scabra*) mimics the local color pattern and threat display of various small vipers inhabiting parts of its range.

Procryptic Coloration

Color resemblance is shown by the correlation of dorsal color and habitat (Lönnberg, 1922). The clearest case is that of *D. m. medici*, individuals of which are pink to reddish in color, as stated by Loveridge (1942, and in conversation) and resemble closely the color of the lateritic soils of coastal East Africa where they are found.

Several forms inhabit grasslands or savannas with sparse vegetation. Among these are the "typically" colored phases of *D. palmarum* (Lower Congo and Angola) and of *D. scabra* (Arabia to the Cape, west to Liberia). *D. inornata* (Natal) may also be included here, because although its ecology is not known, no forest exists through most of its range. All three forms are light brown or tan dorsally. Designs, when present, are traced in black, cream, and various shades of brown, always consist of a row of dorsal saddles with lateral bars, and show many permutations (cf. Gans, 1959, pls.).

The forest forms, *D. fasciata* (principally in western and Central Africa) and "montane" *D. scabra* (from the mountainous portions of the Uganda-Ruanda Urundi-eastern Congo region = variety *atra* of Sternfeld), are much darker colored. A small but variable percentage of "montane" *D. scabra* is uniformly light or reddish brown. The light brown specimens may occur with higher frequency at median altitudes where forest patches are smaller, and may reflect an intermediate ecological condition. Series collected in high (6,000+′) montane forest are entirely black (20%; $N > 100$) or black and dark olive brown. In striking contrast, no melanistic specimens occur in the "lowland" samples of *D. scabra* or in samples of the other species. *D. fasciata* also varies from dark olive to brown dorsally. All specimens of *D. fasciata* and up to 65% of some samples ($N > 100$) of "montane" *D. scabra* give the impression of a broken pattern or a dorsal mottling of the base color. In *D. fasciata* this is a relatively clear pattern on the interscalar skin alone, while the "montane" specimens also have a washed-out or "faded" pattern on the external surface of the scales. The latter pattern is distinctly accentuated when the body is inflated.

The three general color schemes appear to be closely related to the prevailing tone of the general habitat. The proof for this correlation seems clear in *D. medici*, but the light coloration of the savanna species and the more somber hues of the forest forms are related to the differences in illumination in these two habitats. Further evidence for a correlation between dorsal shade and substratum color is shown by the population of *D. scabra* from Southwest Africa (race *loveridgei* Mertens), in which a general fading of the color pattern accompanies the high light intensity of a semi-desert region.

[2] Virtually nothing is known of the habits of the Indian "egg-eater" *Elachistodon*.

Any of these cases could be cited to support Cowles (1958), whose restatement of Gloger's rule (1833) suggests that there is a gradient of decreasing pigmentation from areas of high to those of low humidity. In most cases, separation of the effects of humidity and the color of the substratum is difficult, but Cowles summarizes evidence that may indicate that substratum color is the controlling factor in open areas.

As for obliterative shading, the ventral surface in all species of *Dasypeltis* is lighter in color than the dorsal, and in forms where dark stippling is present the stipple is less dense close to the margin between the dorsal and ventral scales. Small dark spots, interspersed between the ventral ends of the lateral bars, mark this margin in some of the patterned forms and seem to enhance the simple countershading and further break up the shadow zone.

All but two of the open-country population of *Dasypeltis* show some pattern. Exceptions are the unicolored northern race, *D. medici lamuensis*, the unicolored phase of *D. palmarum*, and *D. inornata*.

All specimens of lowland *D. scabra*, *D. palmarum* and southern *D. medici* possess a pattern of dorsal saddles and lateral bars or blotches, often sharply defined with dark pigments. These markings produce a disruptive effect which, in many cases, is lightened by marginal tone contrasts. Thus, the saddles of *D. scabra* become darker radially from the center towards an edge of black, which is set off by a very light peripheral band that gradually darkens towards the ground color. A variety of cross bars and arrow-shaped V's disrupts the outline of the head.

A much less distinct pattern, reduced to a mottling or marbling of the dorsal color, is present in all specimens of *D. fasciata* and in more than 60% of the "montane" *D. scabra*; it is not disruptive but minimizes the contrast in texture between snake and the substratum.

Warning Reactions

The snakes of the genus *Dasypeltis* engage in threat displays (Gans and Richmond, 1957). These involve inflation of the body, which is held in a characteristic C-shaped coil, coupled with a simultaneous rubbing of adjacent loops. The inclined, serrate keels of the lateral scale rows, when shifting the coils brings them together, produce a hissing or stridulation. The inflation of the body, particularly of the neck, spreads the scales, thus emphasizing the dark pattern markings. Some individuals also spread the posterior tips of the quadrate bones, which gives the appearance of a more triangular or viper-shaped head. The snake strikes repeatedly, and the opposite motion of adjacent body loops breaks up its outline and allows only occasional glimpses of short sections of the pattern and no indication whatever of the proportions of the body.

The over-all effect of this behavior, with the snake in a tight swirling coil, is spectacular, and a "threat" definitely seems to exist, bluff though it may be. Curry-Lindahl (1956) reports an attack by a pair of tits (*Parus fasciventer*) on a specimen of "montane" *D. scabra* surprised in a tree. The birds engaged in the harassment typical for driving off large or potentially dangerous animals, and the snake kept them at a distance by short darts and a loud "hissing." The observer did not see the outcome for he collected the snake after it had successfully descended from a height of 10 feet. It seems clear that the snake's behavior kept the birds at a distance. Without some protective device the reptile would probably have been pecked to death.

Mimicry

History. A considerable body of evidence indicates that warning behavior may be reënforced by mimicry. Several authors comment on the resemblance between various populations of *D. scabra* and the local species of small vipers. It is noteworthy that the reports list different models (of various genera) for different regions. Thus *Dasypeltis* is said to resemble *Echis carinatus* in Egypt, Upper Egypt, and Ethiopia (cf. Anderson, 1898; Sternfeld, 1908, 1910, 1913; Rose, 1929, 1950), and the Togo (= Ghana)

region (Werner, 1902; Sternfeld, 1908, 1910, 1913; and Scortecci, 1939, who does not refer to a specific locality), *Causus rhombeatus* in Tanganyika and South Africa (Weale, 1871; Lönnberg, 1907; Loveridge, 1918, 1928; FitzSimons, 1919; Rose, 1929, 1950), the young of *Vipera superciliaris* in Tanganyika (Mwaya; cf. Loveridge, 1933), *Bitis arietans* in Mozambique (Tete, Boror; cf. Peters, 1882), *Bitis atropos* in South Africa (Wallace, 1867; Sternfeld, 1913), and *Bitis caudalis* in Southwest Africa (Werner, 1902; Sternfeld, 1908, 1910, 1913; Rose, 1929, 1950; Mertens, 1955).[3] Sternfeld (1910) also interpreted the shorter tail length of the Southwest African *D. scabra* as a *Gestalt* mimicry of the relatively stouter, shorter-tailed *Bitis caudalis*.

Werner (1909, p. 514) expressed disagreement with Sternfeld's views stating that the supposed resemblances were wholly fortuitous. He also would not accept any case of mimicry not based on experimental evidence. Loveridge (1928) and Rose (1929) observe that the "mimics" are often found at localities where the models do not occur. Mertens (1955, p. 115) doubts that the situation (in Southwest Africa) involves real mimicry, as the habitats of "model and mimic" seem quite distinct.

An examination of the patterns of several of these vipers confirms the existence of striking similarities, most notably when comparisons are made with specimens approximately the size of adult *Dasypeltis*, i.e., with juveniles of some of the larger species of vipers. These comparisons also indicate that the similarities extend over the entire range of two species of *Dasypeltis*, and are not limited to particular regions as might be inferred from the literature. They also confirm previous observations that the degree of similarity is not constant over the range of any species of *Dasypeltis* and that the ranges of no two species considered here are coextensive.

[3] Supposed parallels involving wide geographical separation of models and supposed mimics have not been listed.

Observations. Unfortunately no comprehensive work delimits the ranges of the African viperids, or provides detailed descriptions of their systematic status or the geographic variations in their color patterns. The impracticability of engaging in a familial revision at the present forced my proceeding haphazardly. Comparisons of patterns are based on all small African vipers (800+ specimens compared with 1,000+ specimens of *Dasypeltis*) in the collections of the American Museum of Natural History, California Academy of Sciences, Museum of Comparative Zoology and United States National Museum, as well as representative samples from several other collections.[4] General statement regarding viperid color patterns refer to this sample. Published illustrations and color descriptions from life were utilized whenever possible, because postmortem color changes and the often poor preservation of specimens may obscure or alter original color patterns. Only the clearest cases of similarity could thus be commented on.

No concerted search of the literature was made, and many cases may have been overlooked. Furthermore, the often quite approximate locality data allowed no nicety of ecological or even geographical correlation between the collecting site of one individual and that of another.

To avoid some of the dangers inherent in the use of museum material, drafts of the present paper were circulated to various individuals familiar with these animals in

[4] The following species were employed in this study. The identifications are those found on the museum specimens and were confirmed only for material that exhibited pattern similarity with *Dasypeltis*: *Aspis cerastes*, *A. vipera*; *Atheris barbouri*, *A. ceratophorus*, *A. chloroechis*, *A. katangensis*, *A. n. nitschei*, *A. n. rungweensis*, *A. s. squamigera*, *A. s. anisolepis*; *Atractaspis aterrima*, *A. bibroni*, *A. corpulenta*, *A. dahomeyensis*, *A. heterochilus*, *A. irregularis* (incl. *i. katangae*), *A. microlepidota* (incl. *i. phillipsi*), *A. rostrata*; *Bitis arietans*, *B. atropos*, *B. caudalis*, *B. cornuta*, *B. gabonica*, *B. heraldica*, *B. inornata*, *B. nasicornis*, *B. peringueyi*; *Causus defilippii*, *C. lichtensteinii*, *C. resimus*, *C. rhombeatus*; *Echis carinatus*; *Vipera hindii*, *V. superciliaris*.

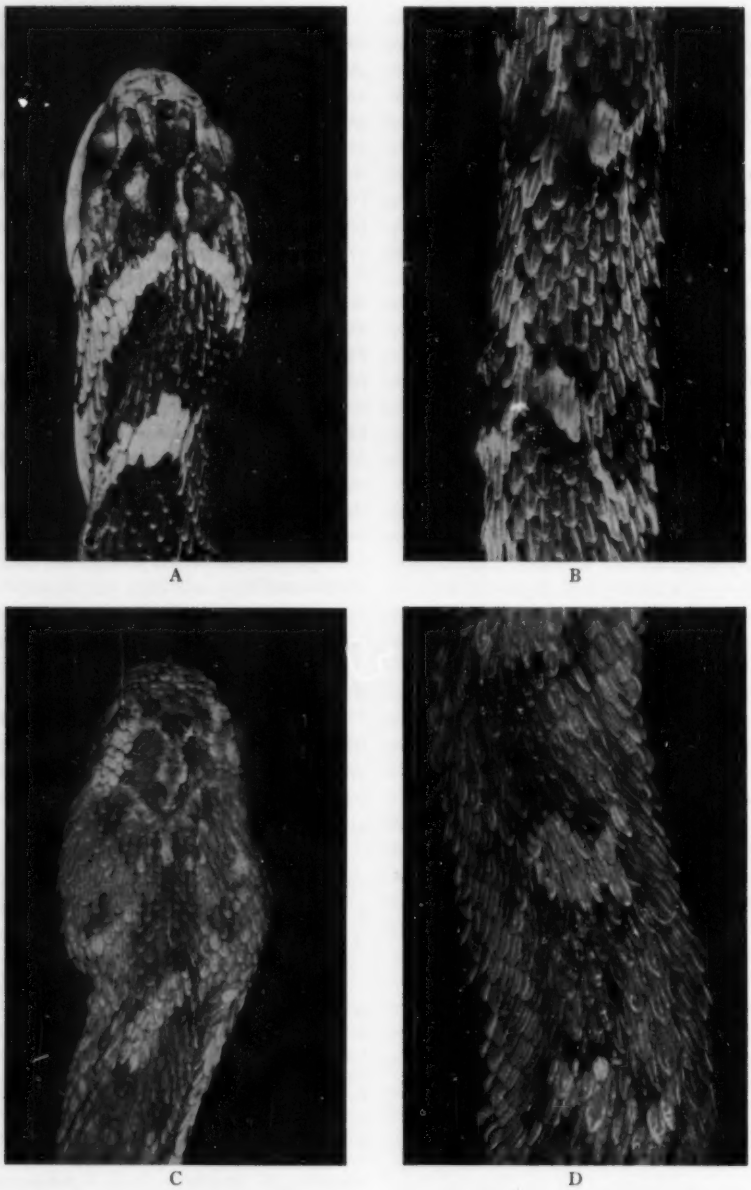


PLATE 1. A. *Dasypeltis scabra*, "Egypt," (Z.M.U. 5865). Head, with faint mottling, first V on nape. B. Midbody region of same specimen showing elongate hourglass-shaped saddles with washed-out lateral margins. C. *Echis c. carinatus*, Cairo, Egypt, (C.A.S. 38722). Top of head mottled, no cephalic V. D. Midbody region of same specimen. The serrated and inclined scales can be seen on both sides.

the wild. Their comments are cited below.

Similarity of coloration. All species of vipers examined were unicolored or had dorsal saddles and lateral bars; none was striped. Many had a prominent V-shaped mark on the head or in the nuchal region. The surface-dwelling species (i.e., excluding the burrowing vipers of the genus *Atractaspis* and some of the green tree vipers) all showed a resemblance in color to that of the substratum, similar to what is described above for *Dasypeltis*. The pattern of dorsal saddles and lateral bars plus the strong resemblance to the color of the substratum produce an initial impression of similarity in any given region, not only between *Dasypeltis* and a particular viper, but also among the various species of vipers.

In the rainforest regions of the Cameroons and the Belgian Congo such similarity exists between *D. fasciata* and *Atheris s. squamigera*, while *D. fasciata* and *Causus rhombeatus* are also similar to each other in rainforest regions of Liberia and the Cameroons. The marbled or mottled "montane" specimens of *D. scabra* are similar in tone to *Causus lichtensteinii* in the Ruanda Urundi region. *Causus rhombeatus*, *Atheris squamigera anisolepis*, and *Dasypeltis palmarum* show a parallel pallor in the Lower Congo region. While mimicry may be involved, it need not be predicated, because the several species are in each case under the action of the same selective force.

Variation of color pattern in Dasypeltis *and possible models. Dasypeltis*: Of the five species in the genus, only *D. scabra* and *D. palmarum* show a sufficient pattern resemblance to viperine species to deserve discussion.

D. scabra is distributed in savanna regions from Egypt and Arabia to the Cape of Good Hope and west to Gambia (along the southern edge of the Sahara). It is absent in the lowland forests of West and Central Africa, in deserts, and in Angola. Almost all specimens are patterned (cf. p. 73). Only a very small, geographically variable, percentage of unicolored specimens has been recorded. (The "montane" phase of *D. scabra* is omitted here.) The geographic variation of dorsal pattern elements is shown in figure 1. This diagram overstates the extent of regional variation, because the extremes of local trends are emphasized in illustration.

D. palmarum occurs in a similar habitat from the French Congo through Cabinda, and the Lower Congo region, to Central Angola. Three-quarters of the specimens are patterned; the remainder are unicolored brown dorsally. The pattern consists of extremely small, dorsal, rhomboid saddles, often apparent only as a middorsal widening of the fusing lateral bars. *D. scabra* and *D. palmarum* may be sympatric in the Lower Congo region.

The horned vipers—*Aspis cerastes* and *A. vipera* (*Cerastes* sp. of authors): These small species are restricted to the north African and Arabian deserts, and their ranges overlap that of *Dasypeltis* only in Egypt. They both exhibit a pale dorsal ground color, on which is superimposed a pattern of small, square, dorsal saddles, with two rows of alternating triangular lateral bars or dots. Neither species has a nuchal or cephalic V. There is a slight resemblance between the general pattern of *Dasypeltis* and that of *A. cerastes*, but it is not nearly so strong as that between the local *Dasypeltis* and *Echis carinatus* (see below).

Both species of *Aspis* are sidewinders, and have rows of serrated lateral scales used in a stridulating warning mechanism similar to that of *Dasypeltis* and *Echis*. The modified lateral scales apparently assist *Aspis* in covering itself with sand (Schmidt and Inger, 1957). The venom of this genus is stated to be extremely potent.

The rhombic night adder—*Causus rhombeatus*: This variable species is as widely distributed as *D. scabra*, but, unlike the latter, does not occur in the low-rainfall regions of Arabia, Egypt, western South Africa, and Southwest Africa. It does invade the lowland rainforest of the Congo Basin and West Africa (where *D. scabra* is absent) and ranges farther north in the west, to Mauretania (Loveridge, 1957). It feeds on frogs

FIG. 1. Map showing some of the more conspicuous geographic variations in the shape of the dorsal saddles of *Dasypeltis scabra*.

and toads, hence frequents moist regions. Though the various species of *Causus* are much more slender than those of *Bitis* or *Echis*, *C. rhombeatus* is rather stouter than *D. scabra*. Apparently an ontogenetic change occurs in the color pattern. All comparisons were made between specimens of the same girth.

The pattern consists of saddles and lateral bars of dark brown, countershaded in cream on a light brown ground. Patterned specimens have a broad V-shaped marking on the nape. Some specimens have a faint pattern or are unicolored. The considerable variation in the material examined by me seems to be attributable to ontogenetic changes, or to ecological, and geographical influences. Thus the pattern fades out in adult specimens; the markings remain apparent only across the edges of the scales. Samples collected in lowland rainforest contain specimens with a much darker and more diffuse pattern and a higher frequency of unicolored individuals. Geographic variation is shown by a variety of saddle shapes and relative sizes and differences in the frequency of unicolored specimens.

C. rhombeatus "coils" and strikes vicious-

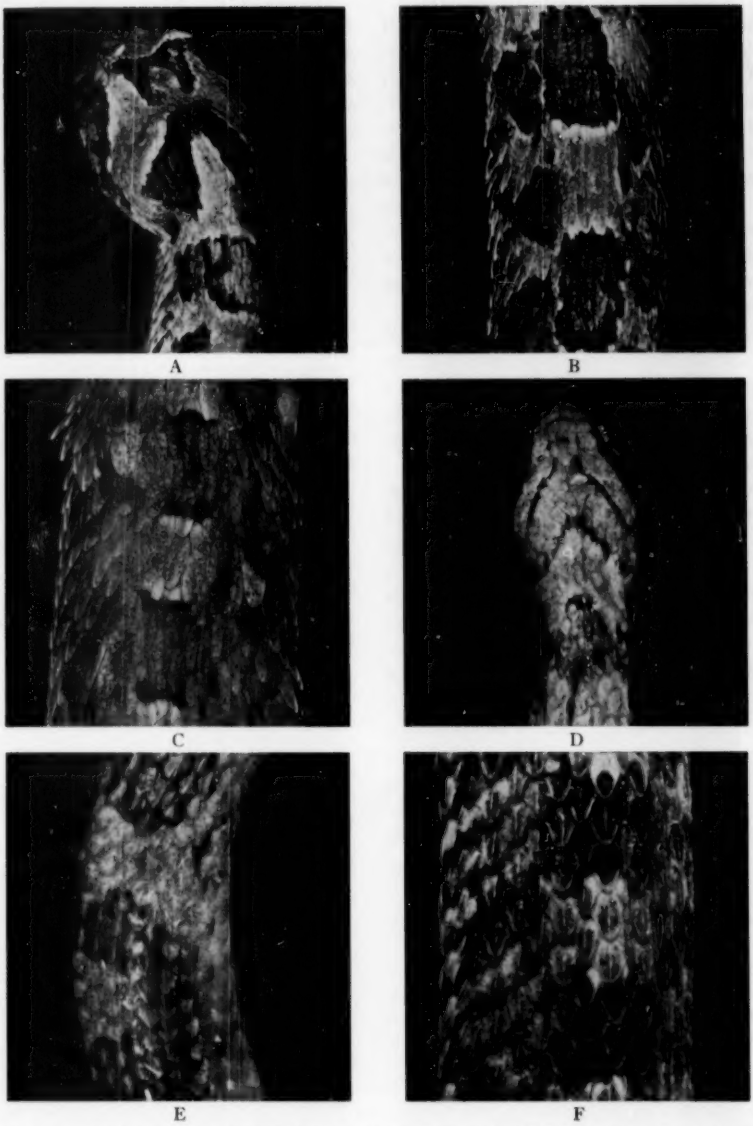


PLATE 2. A. *Bitis caudalis*, Zoutpansberg, Northern Transvaal, (M.C.Z. 14192). Head of specimen from eastern part of range showing V on head. Some of the scales in the region of the first saddle have peeled, reducing contrast and indicating the extent to which this is affected by preservation. B. Midbody view of same specimen. C. *Bitis caudalis*, Mossamedes, Angola (C.A.S. 86646). Midbody view to demonstrate lightening of pattern, squarish saddle shape and lack of lateral margins to the saddles. D. *Causus rhombeatus*, "Matabeleland," Southern Rhodesia, (A.M.N.H. 5815). Head of poorly preserved adult showing central fading of the pattern units. E. Midbody view of same specimen showing peripherally defined hexagonal saddles. F. *Dasypeltis scabra*, Windhoek, Southwest Africa, (S.M.F. 41928). Midbody pattern for comparison with figure C.

ly, launching its body almost entirely off the ground (Loveridge, 1928; Broadley, 1957). In some regions (i.e., the Transvaal; Brain, *in litt.*) these adders characteristically engage in a series of ill-directed strikes, with the mouth closed, as *Dasypeltis* is known to do. The vipers may also inflate and flatten the body bringing the pattern more sharply into view. Opinions differ regarding the toxicity of the venom, but it is presumed not to be highly toxic to man or large animals (Pitman, 1938).

Considerable variation exists in local populations of the viperids seen by me, but the pattern of *D. scabra* from the eastern half of Africa (Sudan, Uganda, and Kenya, to Natal) closely resembles that of *C. rhombeatus* from the same areas.

Most Nyasaland night adders are recorded from hilly forested localities and show a darker and more diffuse pattern than *D. scabra* from the lowland savanna. A single specimen of *D. scabra* from the Nyika Plateau has a diffused pattern similar to that of local *C. rhombeatus*.[5] Some "non-forest" records from the Congo and those from the Ghana region (where a break in the coastal forest belt allows savanna species such as *D. scabra* to approach the coast) also include egg-eaters and night adders with similar patterns. The lateral bars are found "linked" to the saddles (see fig. 1) in most West African individuals of each species.

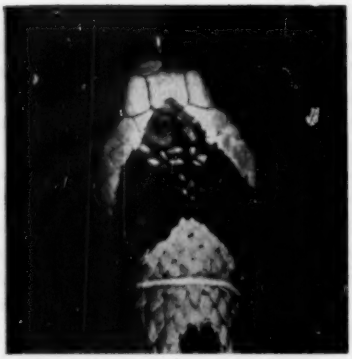
An interesting phenomenon is the presence of unicolored specimens of *D. scabra* in several regions where the night adder also has a unicolored phase. One such area is the Umtali-Odzi region of Southern Rhodesia (Broadley, 1957; FitzSimons, *in litt.*). All other specimens of *D. scabra* from Southern Rhodesia are patterned, but the unicolored *Causus* is said to be fairly common in the northern half of the country and in Northern Rhodesia (Broadley, *in litt.*).

The only Lower Congo specimen of *C. rhombeatus* seen by me has the cephalic V and the light, narrow, linked, dorsal saddles that characterize *D. palmarum*. Other specimens of *C. rhombeatus*, from inland southern Angola, do not resemble coastal *D. palmarum*, but no *Dasypeltis* from the inland area has been examined. The specimens of *C. rhombeatus* have a pattern similar to that of a series of *C. resimus*, from the same region, that were a "dull greenish brown" in life (Bogert, 1940). Monard (1951) mentions unicolored night adders from "Angola."

The snouted night adder—*Causus defilippii*: The range of this species extends from Kenya to Natal and inland to the Rhodesias. The dorsal color of alcoholic specimens is brownish, and the pattern is similar to that of *C. rhombeatus*, but sharper. *C. defilippii* is not so large as *rhombeatus*. The dorsal saddles are roughly hexagonal except for the posterior edge which may be sharply delineated. The lateral bars join the saddles. There is a marked nuchal V. All dark pattern elements are countershaded with light tan. Loveridge (1953) reports unusual dark green Nyasaland specimens. *C. defilippii* and *C. rhombeatus* appear to replace each other locally (Broadley, 1957) in

[5] A similarity difficult to assess, because there are no undoubted highland forest records for *D. scabra* from Nyasaland. The recently accelerated deforestation of this area further complicates the issue.

PLATE 3. A. *Causus defilippii*, Liwale, Tanganyika Terr. (M.C.Z. 53025). View of head. B. *Echis carinatus pyramidum*, Trachura Training College, Naurongo, Ghana (M.C.Z. 55310). Midbody view. Note elongate saddles and light spot in center of lateral bar. C. *Bitis heraldica*, Micado de Dondi, Bella Vista, Lobito, Angola (M.C.Z. 32489). Midbody view of peeled specimen. Note the sharp contrast of the middorsal stripe. D. *Dasypeltis scabra*, Mpwapwa, Tanganyika Terr. (Z.M.U. 13304). View of head showing multiple V's. E. *Dasypeltis scabra*, Accra, Ghana (Z.M.U. 6431). Midbody view. Note elongate saddles and the manner in which the lateral bars approach, but remain discrete from, the saddles, thus approximating the appearance of the light spots shown in figure B. F. *Dasypeltis palmarum*, Vista, Lower Congo (R.G.M.C.). This specimen is much thinner than the *B. heraldica* shown in figure C. Its entire width resembles the central strip of the latter.



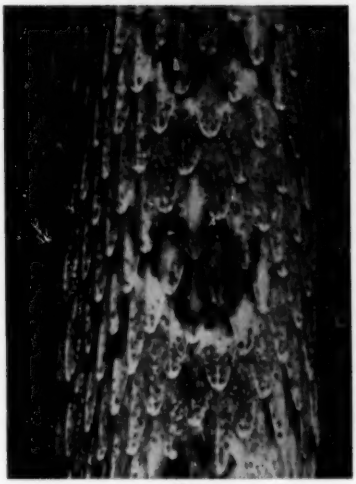
A

B

C

D

E



F

Southern Rhodesia. Their habitat requirements seem to be similar, *C. defilippii* preferring moist lowland regions and *C. rhombeatus* higher areas (C.J.P. Ionides, *in litt.*, for Tanganyika).

C. defilippii serves as a possible model for *D. scabra* which occurs throughout its range. The general impression of similarity is great in spite of the above-mentioned differences in pattern detail.

Causus lineatus: Laurent (*in litt.*) points out that this species of the savanna and high plateaus of the eastern Congo has the same color pattern as *C. rhombeatus*, but is more slender. It thus forms an even better model for the local *D. scabra*.

The horned adder—*Bitis caudalis*: This thick-bodied, short-tailed species is found in the relatively more arid regions of Southern Rhodesia and southwestern Africa from Angola to the Cape Province (Mertens, 1955). The males exhibit both a semblance of a cephalic V and a series of dorsal saddles (Broadley, 1959). The entire pattern is subject to degrees of fading, being in females almost indistinguishable from the dorsal ground color (Rose, 1950, fig. 195). The pattern of the males apparently shows a geographic gradient in the shape of the saddles. Among Southwest African specimens (including those figured by Mertens, 1955) rectangular, middorsally constricted, blotches predominate. The saddles lack lateral margins; only the front and rear edges are sharply defined. A more northern specimen from the Kaokoveld region has this pattern posteriorly, but the anterior saddles are hexagonal. I have only seen a few Southern Rhodesia and Transvaal specimens. These had hexagonal saddles with lateral margins, thus resembling *Causus rhombeatus* (and *D. scabra*) from the same region.

In Southwest Africa *B. caudalis* is found in divers habitats, from sand and stone desert to dense bushveld (Brain, *in litt.*) and appears to serve as a model for *D. scabra* wherever the two occur together. It is noteworthy that the geographic gradient in the viperid pattern is closely paralleled by that in the egg-eaters. Almost all specimens of *Dasypeltis* from Southern Angola, and the southern area and central massif of Southwest Africa (var. *loveridgei* Mertens) have square saddles with some middorsal constriction. Those from the Waterberg region have irregular hexagons, while Rhodesian specimens have the regular hexagonal pattern. The marked resemblance of central Southwest African specimens of *Dasypeltis* to the local form of *Bitis caudalis* has been pointed out repeatedly (cf. p. 73).

Another noteworthy resemblance is the relatively shorter tail in the Southwest African population of *D. scabra* (Gans, 1959, fig. 24). The tail of these egg-eaters is proportionally the shortest within the genus. An apparent gradual decrease in tail length from the Rhodesias westward to Southwest Africa may be correlated with the distance from the range shared with *C. rhombeatus*, or with the distance into the range of *B. caudalis*. The horned adder has a much stouter body and shorter tail than either the night adder or the egg-eater. Sternfeld (1910) suggests that the shorter caudal length of *Dasypeltis* in Southwest Africa is shape mimicry, with *B. caudalis* as model.

B. caudalis can move rapidly by sidewinding across sand and can cover the body with sand. During this process it lies in a C-shaped coil, similar to that assumed by *Dasypeltis* when resting or engaging in warning behavior. The vipers strike rapidly and repeatedly when disturbed and produce intermittent loud hissing noises (Mertens, 1953, 1955). The venom of this species is said to be far less deadly than that of *B. arietans* (Rose, 1950).

Bitis heraldica[6]: I have seen only three specimens of this Angolan form. These (from Mombolo and Bella Vista) show a light middorsal band enclosing diamond-shaped areas delineated by narrow, dark, faintly countershaded lines. There is a V-shaped marking on the nape. The light middorsal band is flanked by a darker band on each side, and this, by a dark zone that con-

[6] The status of this species is discussed by Hellmich (1957) and Mertens (1958).

trasts sharply with the central area. These snakes are much stouter than *Dasypeltis* and lack lateral bars, yet the whole pattern of a *D. palmarum* from Caconda agrees well with the pattern of the middorsal zone of the vipers. Caconda is one of the few inland Angola localities from which I have seen a *Dasypeltis*; the pattern of which differs from that of *D. palmarum* from coastal localities, but more closely resembles that of certain variants of *D. scabra*.

The saw-scaled viper—*Echis carinatus*: In Africa this species occurs in arid areas from North Africa southward to northern Kenya and Uganda and westward to Ghana. The pattern of eastern (Egypt to Kenya) specimens is comprised of middorsally constricted, longer than wide saddles, that are widest at their midpoint and have poorly defined lateral borders. The head is dark, without a nuchal or cephalic V. Specimens from western Nigeria and Ghana, considered by Loveridge (1957) possibly to be distinct taxonomically, have shorter, more squarish to hexagonal, saddles with linking or alternating lateral bars. In western specimens, a pair of short, posteriorly diverging stripes on the top of the head give the superficial impression of a poorly defined V.

The pattern on the body of eastern specimens is almost identical with that of *D. scabra* from Egypt, the northern Sudan, and northwestern Ethiopia. The pattern of western specimens closely resembles that of *Causus rhombeatus* and that of *D. scabra* in the Ghana region. A further parallel is furnished by the pattern on the head. Egyptian and northern Sudan specimens of *D. scabra* are unique among East African populations in having a dark, but completely unpatterned cephalic surface (Gans, 1959, pl. 4, figs. 5–6), while West African *D. scabra* always have a marked cephalic V. This is in good accord with the hypothesis that *E. carinatus* serves as the model.

E. carinatus is a sidewinder with serrated lateral scales that serve for noise production. The species characteristically coils in a C-shaped loop like that described above for *Dasypeltis*. The saw-scaled viper's aggressiveness and potent venom "make it one of the most dangerous of all venomous snakes" (Schmidt and Inger, 1957).

The lowland viper—*Vipera superciliaris*: This species is of limited distribution and extremely rare in collections. It has been recorded from southwestern Tanganyika and from Mozambique (Loveridge, 1957). It has a cephalic V and a series of large, hexagonal, middorsal saddles. Lateral to these are broad blotches or triangles producing an over-all impression of a series of cross bands rather than discrete saddles and bars (see Cott, 1935, pl. 1). The markings are striking and are reminiscent of *D. scabra*, but the similarity is not close enough for this viper to be considered a model without further evidence.

Regional summary. A restatement of the situation in geographic terms is given below, and figure 2 shows the ranges of possible models of *Dasypeltis scabra*. Proceeding around Africa in a clockwise direction from the north, we find that in Egypt and the northern Sudan *D. scabra* is similar to *Echis carinatus*; in Uganda, Kenya, Tanganyika, Nyasaland (?), Mozambique, the Transvaal, and Natal, to either *Causus rhombeatus* or *C. defilippii*; in the Rhodesias, to the forms of *Causus* and *Bitis caudalis*; in Southwest Africa, to *Bitis caudalis*; in the highlands of central Angola, possibly to *Bitis heraldica*; in the Belgian Congo, to *Causus rhombeatus* and *C. lineatus*; and in the Nigeria-Ghana region, to *Causus rhombeatus* and *Echis carinatus*.[7]

Dasypeltis palmarum is similar to *Bitis heraldica*, though the relative ranges of the two species cannot be delimited at present. The incidence (approx. 25%) of unicolored specimens of *D. palmarum* suggests that mimicry involves only a single phase of this polymorphic species.

The mimicry extends a step beyond the pattern, as *Dasypeltis* shares not only the color pattern but the warning behavior of the vipers. Although the use of serrated

[7] Mertens (*in litt.*) says that *Bitis worthingtoni* may be another East African model, but I have not examined specimens.

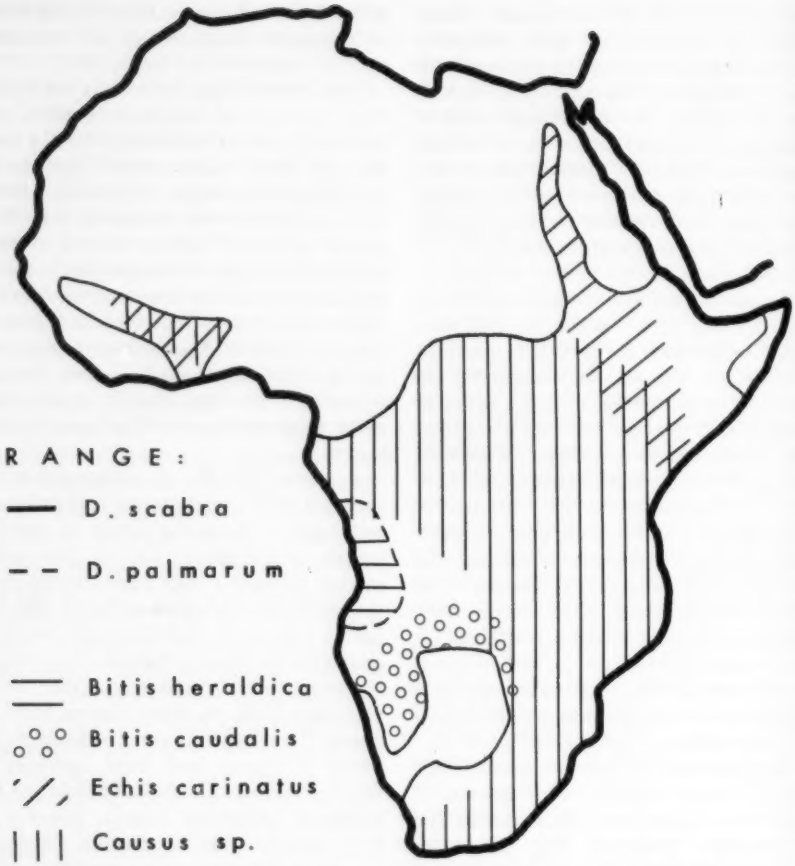


FIG. 2. Distribution of 2 species of *Dasypeltis* with ranges of presumptive models for the various areas discussed. The gap in the Cameroons-Nigeria region is probably artificial.

scales for sound production is noted only in *Dasypeltis*, *Aspis*, and *Echis*, the other species of vipers also use a moving coil superficially similar, hiss loudly, and strike actively and repeatedly.

Figure 2 gives only an approximate indication of the scattered nature of the material examined. It should be remembered that some of the gaps are due to the ecological preferences of the collectors rather than of the animals.

ARGUMENT

Statement. The preceding account lists several cases of similarity between the pattern of *Dasypeltis scabra* (possibly of *D. palmarum* also) and that of one or more of the vipers. These cases extend over the entire range of *D. scabra* in the savanna. The similarity is restricted in that the mimic more closely resembles the local model than specimens of the model species from areas geographically farther removed. Also interesting are the situations in which several vipers in the same area have the same or closely similar patterns. For the sake of the argument these situations are tentatively interpreted as instances, of Batesian and Müllerian mimicry, respectively.

Various arguments have been raised against the mimicry hypothesis, many of which Hecht and Marien (1956) and Mertens (1956) have effectively answered in their discussion of the "coral snake mimics." I accept their general arguments for the existence of mimicry in snakes, and here only arguments specifically pertinent to the present case are discussed. In my opinion similarities are not the result of parallelism, accident, the effect of a "genius loci," or orthogenesis (cf. Mertens, 1956).

Wallace (1867) presented five conditions for a model-mimic situation: (1) sympatry of model and mimic, (2) difference of the mimic from its relatives, (3) restriction of the mimicry to external characters, (4) fewer mimics than models, and (5) the mimics have less ability than the models to defend themselves. Two other important factors are (a) the bearing of the lethality of the model's defense on the learning process of possible predators, and (b) the differences in body proportions among the various forms involved. Finally there is the crucial question of whether the patterns are cryptic only or represent "true warning" coloration.

Sympatry of model and mimic. Coextensive distributions: This condition for mimicry cannot be applied absolutely. Diversity in modes of life suggests that the distributions of most species depend upon a complex interplay of environmental factors. The egg-eaters are markedly successful as a genus, and *D. scabra* is certainly the most widespread species. Savanna habitats seem to fill its general ecological requirements. The range of *D. scabra* appears to be limited by the egg diet, though to what extent *Dasypeltis* depends on the eggs of tree-nesting as opposed to ground-nesting birds is unknown.

The species of *Causus*, the presumed models over most of the range of *D. scabra*, feed exclusively on frogs and toads, which may explain why they have not invaded the drier regions of Africa. That *Dasypeltis* substitutes another model only when *Causus* is absent is strong presumptive evidence for Batesian mimicry.

The "switching" of models is facilitated by what is interpreted here as Müllerian mimicry between the several models through zones of overlapping ranges and explains the similarity between *C. rhombeatus* and *B. caudalis* in western Rhodesia and between *C. rhombeatus* and *Echis carinatus* in eastern Ghana.

Ecological concordance: Distinct habitats are important only in relation to the ecological preferences of possible predators (plus the nesting birds in the case of *Dasypeltis*). Several ecological zones often interdigitate or form mosaic patterns, the islands of brush or scrub forest (inhabited by *Dasypeltis*) surrounded by desert (inhabited by *Bitis caudalis*) in Southwest Africa, and the similar conditions in Egypt for examples. The range of the prey is not necessarily affected or delimited by the same influences determining that of a predator, especially if the latter is a carnivorous mammal or raptorial bird.

The presence of *Dasypeltis* in limited areas of scrub forest, surrounded by ecologically unsuitable terrain inhabited by its model, would actually be ideal for meeting Wallace's fourth condition for mimicry, i.e., there must be fewer mimics than models. Predators, nesting birds or both, were they to range from scrub to dry area, would have an excellent opportunity to encounter the model. Any increase in similarity would then be of selective advantage to the mimic.

Difference of mimic from its relatives. The isolated phylogenetic position of *Dasypeltis* makes this condition of doubtful relevance.

The five species of *Dasypeltis* are apparently very closely interrelated, yet, though all patterned species show variations of one arrangement, the pattern of *D. scabra* is distinct.

It is difficult to explain the presence of a warning mechanism in two of the "nonmimicking" species (*D. medici* and *D. fasciata*). Although the behavior has never been reported in the latter, its existence may

be deduced from the presence of modified lateral scales. However, the problem may be partly semantic. Such lateral serration originated independently in the Dasypeltinae and in the Viperidae and seems to be restricted to these two groups. Unpublished evidence (D. Dwight Davis, in conversation) indicates that *Aspis* uses its lateral scale rows to "shovel" its way into loose sand, so that the warning mechanism may be a secondary utilization of an existing structure. In *Dasypeltis* the threatening function appears to have been primary. In view of the magnitude of the modification and of the close relationship of the species within the genus, it is not astounding that they share this characteristic, particularly as the behavior is likely to have a deterrent effect *per se*, regardless of whether mimicry is involved. Probably the most primitive species of the genus, *D. inornata*, has the least lateral modification.

Restriction of mimicry to external characters. Obviously the mimicry must affect characteristics that can be observed by a predator. The vipers and the egg-eaters show such fundamental differences in internal anatomy that they are placed in different families.

Relative frequency of mimic and model. Only field records are pertinent on this point because representation of the species in museum collections is affected by too many variables. Two sets of field records, both for southern Africa, are available. Brain (*in litt.*) reports that *Causus rhombeatus* is at least twice as common as *Dasypeltis* in the Krugersdorp area of the Transvaal, while Broadley (*in litt.*) mentions a ratio of approximately ten specimens of *Causus* (*rhombeatus* plus *defilippii*) to one of *Dasypeltis* in Southern Rhodesia.

The lethality of the defense mechanism. That any viper is better able to defend itself than is *Dasypeltis* hardly requires demonstration. The objections have come from another direction.

Various discussions of mimicry in coral snakes have mentioned the lethality of the venom as a major difficulty to belief in mimicry. If the bitten animal is certain to die, it could not learn the warning pattern. The relative lethality of the venom, of course, depends on the animal bitten, as studies tend to suggest that snake venoms are often quite specific. Their primary function concerns food capture and predigestion, and they are more effective against food organisms than against predators. The difficulty may also be considered minor in the present case, because several of the vipers belong to smaller species and their venoms are not of the most virulent type, with the obvious exception of *Echis carinatus*. While a full bite of most of the species might kill or severely cripple many predators, others might survive if only one fang penetrated, or both fangs might be deflected by the feathers or the bony legs of birds, so that a "lesson" could be learned.

Learning need not be involved. Selection could favor the survival of behavioral traits that lead animals of one species to react in a stereotyped fashion to the presence of others —or their mimics. Thus rattlesnakes from areas where no kingsnakes occur assume the defense posture in the presence of kingsnakes (Bogert, 1941). On the other hand, an investigation of the learning behavior of social or colonial animals (whether birds or mammals) subjected to repeated losses from snake bite might reveal reactions of value in interpretations of mimicry. Not all birds react in the same way to predators, as shown by Hoesch's observation (*in* Mertens, 1954) of a snake (*Dispholidus typus*) that passed unmolested from nest to nest of a colony of *Philetarius socius*. The lack of concern often noted when individual birds are placed in snake cages as food also leads to considerable doubt about the role of learned versus innate responses in such behavior (see comments by Hediger, 1955).

Differences in body proportions. There is a definite decrease in the relative diameter of the body (body diameter to snout-vent length) from *Bitis* and *Aspis* to *Echis*, *Causus*, and *Dasypeltis*. The argument that such dissimilar animals could not form part of a single model-mimic relation would

carry more weight *if* the predator's recognition depended on body shape.

Recent studies of behavior (Tinbergen, 1948; Crane, 1952) indicate that the characteristics by which animals recognize environmental objects, in this case those indicating danger rather than food, may be specific and apparently insignificant. The shifting coils of *Dasypeltis* break up its outline and allow the predator to catch only occasional glimpses of portions of the color pattern. *Causus rhombeatus* and several of the other vipers engage in similar rapid movements.

Even apparently unicolored specimens of *C. rhombeatus* have the interscalar skin marked so that "the rhombs suddenly appear when the snake inflates its body" (Broadley, 1957). This fact, and the emphasis that is placed on the rhombs of patterned specimens by the act of spreading or inflation, suggest the importance of the pattern elements.

The pattern of the inland specimen of *D. palmarum* appears to imitate only the light-colored middorsal stripe of *Bitis heraldica*. This species, as do several of the larger species of *Bitis*, has central pattern elements that seem superficially independent of the lateral coloration. The central stripe is the most conspicuous. Because the lateral region tends to blend, in tone, into the substratum, the relatively narrow middorsal band produces a visual impression of a slimmer snake. It is this pattern that is replicated by *D. palmarum*, and may compensate for the difference in body diameters of model and mimic.

Another item confirms the suggestion that recognition depends on the pattern rather than the over-all shape of the snake. *C. rhombeatus* seems to undergo ontogenetic variation of color pattern, yet *D. scabra* mimics the pattern of snakes of equivalent girth yet of different body lengths. A specific and constant ratio of pattern element size to body diameter will then be selected for, while the ratio of pattern size to specimen length can vary.

Recognition characteristics may also be furnished by the V-shaped markings on head and nape. The spreading of the quadrate-mandibular articulation exhibited by *Dasypeltis* promotes a similarity of outline between their initially slender head and the triangular head of the vipers. The head and neck are the only regions that remain relatively immobile during the warning behavior. Their pattern thus has a better chance of being perceived and "learned" than that of the constantly shifting trunk.

Cryptic coloration versus mimicry. That either protective coloration or mimicry (of a bright "warning" pattern) must be involved in a given situation has been implicit or explicit, but ill supported with evidence, in many discussions of mimicry. Predators can roughly be divided into two categories: (1) general predators likely to avoid prey that has become associated with a "bad" experience, and (2) specialized predators that are able to counteract the defensive mechanism. As long as they exist, there is some selective advantage in hiding or in being inconspicuous.

The ideal pattern would serve as a warning to generalized predators and be inconspicuous to specialized ones. An alternative would involve display of the warning only to generalized predators and imply some discrimination on the part of the snake, in other words a discrimination between categories of predators *prior* to their attack.

Such discriminatory ability has been demonstrated in snakes (Bogert, 1941) as well as in other animals (Crane, 1952; Tinbergen, 1948), yet its existence is not essential to the present argument. Many predators hunt by sight and show markedly keen recognition of moving objects. Immobility and cryptic coloration may enable an animal to avoid them (Kettlewell, 1956). The close color resemblance of the small vipers to the local substratum indirectly indicates the importance of the cryptic factor in their coloration. Warning or threatening behavior becomes important only *after* the snake has been disturbed, whatever the releaser (of motion by the snake) may have been. The visual and aural cues furnished during

the warning cycle, coupled with the sudden onset of such behavior and the reëmphasis of the color "pattern" (cf. observations of Broadley and others) of certain species, would serve as recognition characters reënforcing one another in the release of a fright or caution reaction in the predator. Rapid and repeated movements *toward* the prospective predator and initiated from a moving coil that tends to obscure the snake's length and outline might also serve to inhibit the attacks of predators.

Because the small vipers are also predatory, feeding on a variety of small tetrapods, cryptic coloration would be selectively advantageous in preventing their prey from detecting their approach.

The arguments for a cryptic plus a warning coloration in the vipers may also be used to explain the crytic coloration plus mimicry in *Dasypeltis*. If the combination of pattern functions protects the model, it should also confer a selective advantage on the mimic.

Part of the problem concerning *Dasypeltis* may lie in finding a deterrent for the various small birds that annoy the snakes, though such birds can not be considered predators. These birds might not come into contact with vipers, if only the egg-eaters frequented the vicinity of nests. However, they might encounter the models while foraging.

Mimicry and Environment

The preceding discussion demonstrates a close correlation between environment, color, and color pattern in local populations of various species of *Dasypeltis*. The mimicry (or close pattern similarity) of *Dasypeltis* to some of the small vipers is restricted to forms living in relatively open savanna or scrub forest. The populations of the dense forest demonstrate less emphasis upon a color pattern, and at least one group ("montane" *D. scabra*) has a high degree of polymorphism in its coloration.

This situation shows an interesting parallel in the models selected by *Dasypeltis*. Thus the ranges of *D. scabra* and of *Causus rhombeatus* and *C. defilippii* overlap extensively, and the two species of *Causus* serve as models throughout the areas jointly occupied. Two kinds of habitat are invaded only by *Dasypeltis*, namely, the higher montane forests and drier sub-desert regions. *Dasypeltis* persists apparently without model in the forest situation, but the egg-eaters utilize the pattern of another local viper in each of the two major "desert" areas. The desert models are *Echis carinatus* in the Sudan-Sahara and *Bitis caudalis* in Southwest Africa. These two mimic-model situations have received most of the attention of earlier investigators, an indication of the remarkable similarity. The shortening of the caudal region of the Southwest African egg-eaters is also the only case of *Gestalt* mimicry in the genus.

These cases lead one to suppose that the selective pressure on external coloration may increase with the relative "openness" of the environment. Furthermore, the nature of the selective forces may vary with the environment. "Sight-hunting" predators would be the major and controlling selective force in open areas with sparse vegetation. Initial matching of body color to the substratum and the presence of warning pattern and behavior might be ascribed to adaptive responses, a conclusion also in accord with the data Cowles (1958) provides. However, this conclusion does not discredit the validity of Gloger's or similar rules in environments where predators dependent largely on visual cues are of little importance and patterns and colorations are the result of other selective forces.

Other Mimics

It has been repeatedly suggested that other forms may be involved in the present scheme. Mention was made of *Rhamphiophis multimaculatus* (Sternfeld, 1908), juvenile *Tarbophis* (=*Telescopus*) *variegatus* (Leeson, 1950), and *Pseudaspis cana* (Hoesch, 1958, 1959) and possibly *Boiga pulverulenta* (Shanin, *in litt.*).

Summary and Conclusions

Many writers have noted that snakes of the genus *Dasypeltis* are similar to and may mimic several species of small vipers in various parts of their respective ranges. This situation has been re-examined.

Dasypeltis is protected in three distinct ways: (1) by the attainment of a procryptic coloration, (2) by a warning mechanism (Gans and Richmond, 1957), and (3) in at least one species (*D. scabra*, and possibly *D. palmarum* as well), by a marked resemblance of the egg-eater's dorsal pattern to that of several small vipers.

The *pattern resemblance* is discussed in detail. Its major features are:

1. *Dasypeltis scabra* is the most wide-ranging species of the genus. It ranges from montane rainforest through savanna to semi-desert areas.

2. Over the savanna part of its range *D. scabra* is sympatric with either *Causus rhombeatus* or *C. defilippii* or with both. The dorsal and nuchal patterns and the warning mechanism of the three forms are remarkably similar in any area jointly occupied.

3. In the dry regions of the western Rhodesias and Southwest Africa, where *Causus* does not occur, *D. scabra* is similar to *Bitis caudalis* in color pattern, warning behavior, and possibly in shortness of tail.

4. In Egypt, the Sudan, and across the Equatorial regions fringing the southern Sahara to Ghana, in a dry belt in which *Causus* does not occur, *D. scabra* resembles *Echis carinatus* in color pattern and warning behavior.

5. Several other cases, such as the similarity to *Bitis heraldica* in Central Angola, cannot be discussed adequately until more material becomes available.

6. The various species of egg-eaters and vipers differ in relative body diameter. Where ontogenetic changes occur in one species similar changes occur in the other (others), especially when individuals of equivalent (absolute) body diameter are compared.

7. The warning behavior makes it difficult to judge the over-all proportions of the snake, because movement obscures the outline and the eye catches only short sections and the shape of the individual pattern elements.

8. There is evidence that several vipers closely resemble one another whenever they are sympatric.

The occurrence of similar patterns and behavior in two distinct families of snakes, is here *interpreted* as Batesian (and possibly Müllerian) mimicry, of essentially procryptically colored animals, for the following reasons:

1. It is doubtful whether any small non-crepuscular snake with a blatant warning pattern could be sufficiently dangerous to discourage all predators it might encounter in an open environment.

2. The observed similarity of the color patterns appears to be directly related to the "openness" of the environment.

3. A motionless procryptically colored animal would be overlooked by a large percentage of predators depending largely upon vision.

4. The importance of the color pattern by virtue of its constancy of shape for a given body diameter and by its emphasis during the warning mechanism seems apparent.

5. The sudden onset of the visual and aural cues when an attacked snake moves into its warning coil tends to prevent or delay its seizure by predators.

6. If the warning color and behavior patterns are of advantage to the model they would also be of advantage to a mimic.

7. The several general and special conditions for mimicry are discussed.

Obviously field work is needed for the local habitat, food habits, and predators of *Dasypeltis* in the several geographic regions to be determined. Simple experiments might be planned to establish:

1. Whether *Dasypeltis* and the local vipers have many predators in common.

2. Whether important predators are deterred by the viperid pattern, shape, or behavior, and

3. Whether such predators differentiate between the local vipers and *Dasypeltis*, and if so, how.

These experiments will provide the real test of the hypothesis presented here.

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INTEGRATION OF THE GENOTYPE IN GEOGRAPHIC POPULATIONS OF *DROSOPHILA PAVANI*

DANKO BRNCIC[1]
University of Chile, Santiago[2]

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Drosophila pavani, Brncic 1957, is a common species in central Chile, and in Argentina along the eastern slope of the Andes Mountains. Its populations are polymorphic for the gene arrangements in the second and fourth chromosomes (Brncic, 1957, 1958). In chromosome II there is a gene order which differs from Standard by two constantly associated inversions (A, B) in its middle part. In the right arm of chromosome IV there exists, besides Standard, a second gene sequence due to the presence of three overlapping inversions (IV-R; A + B + C). Finally, in the left arm of the same chromosome, there is a gene arrangement which differs from Standard also by a complex of three inversions (IV-L; A + B + C). The heterozygotes for these gene orders occur in most of the populations studied with frequencies close to 50 per cent (Brncic, 1957, 1958). This suggests that the inversion heterozygotes are adaptively superior to the corresponding homozygotes.

In *Drosophila pseudoobscura* (Dobzhansky, 1951), *D. willistoni* (da Cunha and Dobzhansky, 1954) and in *D. robusta* (Carson and Stalker, 1947) the frequencies of inversions may show geographic and seasonal changes. When populations of these species are maintained in the laboratory under certain experimental conditions, substantial changes may occur in the frequencies of the different gene orders. The situation in *D. pavani* seems to be different. There is no good evidence of geographic or seasonal fluctuations (Brncic, 1957, 1958, and unpublished data). Moreover, in some of the stocks maintained for more than six years under the usual laboratory conditions, it has been observed that, although the frequencies of inversions suffer some variations, they usually remain high, as in the corresponding natural populations. This seemed to indicate that *D. pavani* represents a single large polymorphic population, not subdivided into geographic races differing in chromosome structure.

However, the adaptive function of the chromosomal polymorphism need not depend on the inversions themselves, but on the polygene complexes which they maintain (Dobzhansky and Pavlovsky, 1958). Polygenes may exhibit two types of balance (Mather, 1943; Lerner, 1958), namely *internal balance*, by means of which certain blocks of genes are adapted to produce superior fitness, and *relational balance*, established between the genes in a pair of homologous chromosomes. The chromosomal inversions are a mechanism for maintaining the integrity of such coadapted genetic systems in the population. The *relational balance* is responsible for the high adaptive values of inversion heterozygotes and for establishment of balanced polymorphism (Dobzhansky, 1955).

There is, however, evidence that, in at least some species of *Drosophila*, the same inversions may carry different polygene complexes in different populations. The high fitness may be lost in the heterozygotes for chromosomes with different gene arrangements coming from distant geographic regions; the genes of one region may not give high adaptive values with the genes from other regions. This has been found in *D. pseudoobscura* (Dobzhansky, 1957), *D. willistoni*, and *D. paulistorum* (Dobzhansky and Pavlovsky, 1958). Thus, natural populations of these and probably of some other species, show not only qualitative and

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[2] Instituto de Biología "Juan Noe." Zañartu 1042. Santiago, Chile.

quantitative differences with respect to the gene arrangements in their chromosomes, but also in the polygenes maintained by each inversion.

Since the above mentioned species are widely distributed and live in different environments, evolutionary divergence at both levels indicated above is not unexpected. The experiments described in the following pages were designed to test the divergence of the polygenes maintained by the inversions in a geographically more restricted species such as *D. pavani*, in which no clear interpopulational differences respecting chromosomal polymorphism have thus far been observed. Experiments were designed to test the hypothesis that hybridization of geographic races of *D. pavani* may bring about a breakdown of the coadapted gene complexes carried by their chromosomes, with a consequent loss of the superior fitness of the inversion heterozygotes.

Material and Methods

In the experiments to be described, five strains of *Drosophila pavani* were employed: *Copiapo*, established in 1957; *Vallenar*, established in 1957; *Arrayan*, established in 1955; *Bellavista*, established in 1954; and *Mendoza*, established in 1956. Each strain originated from more than 50 females inseminated in nature. The strains were maintained in the laboratory in mass cultures. *Copiapo* and *Vallenar* localities are in northern Chile, *Arrayan* and *Bellavista* in central Chile, and *Mendoza* lies on the eastern slope of the Andes, in Argentina.

Periodic cytologic examination of the stocks after they became established showed no appreciable variations in the frequencies of the gene arrangements present in the chromosomes II, IV-R and IV-L (unpublished data of the author). These frequencies remained high, as in most of the corresponding natural populations (Brncic, 1957) even though they have experienced a few small changes. These stocks were used as the controls employed in the present experiments.

The experimental populations were established as follows. Fifty virgin females from the strain representing one locality were crossed to 50 males representing another, and placed in 250 cc milk bottles with the common *Drosophila* food medium. The flies were periodically transferred to new bottles in order to obtain an adequate number of offspring. The progenies from the different bottles were mixed, and the hybrid populations, as well as the controls, were maintained by transferring a similar number of flies from generation to generation to new bottles. A total of 9 crosses were made: *Arrayan* × *Vallenar*; *Arrayan* × *Copiapo*; *Vallenar* × *Bellavista*; *Vallenar* × *Copiapo*; *Copiapo* × *Mendoza*; *Copiapo* × *Bellavista*; *Mendoza* × *Arrayan*; *Mendoza* × *Bellavista*; *Bellavista* × *Arrayan*. The stocks used as controls and the hybrid populations were maintained in duplicate cultures, in a constant temperature room at 24° C.

After ten generations, the salivary gland chromosomes of 100 larvae from each experimental and control culture were examined in acetic orcein rapid preparations.

Results

In table 1 and in the figures, the data are arranged so that the hybrid populations may easily be compared with the corresponding controls. The fourth column of table 1 shows that in each of the nine experiments, the mean numbers of heterozygous chromosomes per individual are lower in the hybrid populations after ten generations than in the respective controls. Statistical analysis proves that in most cases this decrease of the frequency of heterozygotes is highly significant. However, if each inversion is considered separately, it may be seen that the decrease of the frequency of the heterozygotes is not the same in different chromosomes and in different crosses. In three of the nine mixed populations the heterozygotes in the second chromosome have disappeared completely; in five cases the hybrid populations have fewer heterozygotes than both controls; and in the remaining cross (*Bellavista* × *Arrayan*) the fre-

TABLE 1. *Frequencies (in per cent) of chromosomes found in heterozygous condition, and mean numbers of heterozygous chromosomes per individual in different populations of* D. pavani *and their hybrids after ten generations (N = 100)*

Populations	Chromosome II (hetero. for A+B inver.)	Chromosome IV-R (hetero. for A+B+C inver.)	Chromosome IV-L (hetero for A+B+C inver.)	Mean of heterozygous chromosomes per individual
Arrayan	7	65	34	1.06
Vallenar	22	66	70	1.58
Arrayan/Vallenar	0	2	14	0.16
Arrayan	7	65	34	1.06
Copiapo	33	60	57	1.50
Arrayan/Copiapo	1	18	24	0.43
Vallenar	22	66	70	1.58
Bellavista	55	56	53	1.64
Vallenar/Bellavista	0	17	34	0.51
Vallenar	22	66	70	1.58
Copiapo	33	60	57	1.50
Vallenar/Copiapo	1	20	36	0.57
Copiapo	33	60	57	1.50
Mendoza	24	61	65	1.50
Copiapo/Mendoza	0	29	30	0.59
Copiapo	33	60	57	1.50
Bellavista	55	56	53	1.64
Copiapo/Bellavista	2	34	38	0.74
Mendoza	24	61	65	1.50
Arrayan	7	65	34	1.06
Mendoza/Arrayan	5	32	46	0.83
Mendoza	24	61	65	1.50
Bellavista	55	56	53	1.64
Mendoza/Bellavista	14	32	40	0.86
Bellavista	55	56	53	1.64
Arrayan	7	65	34	1.06
Bellavista/Arrayan	7	38	49	0.95

quency of heterozygotes is identical to that of the control population which has the lowest number, *Arrayan* (table 1 and fig. 1).

Comparing the frequency of heterozygotes for the A + B + C gene arrangements on the right arm of chromosome IV, in the interpopulational hybrids and in the corresponding controls, we see that, without exception, the incidence of the heterozygotes is lower in the mixed populations (table 1 and fig. 2). Finally in the left arm of chromosome IV, the frequency of the heterozygotes for the three overlapping inversions has decreased in seven of the nine hybrid populations (table 1 and fig. 3).

DISCUSSION

The agreement of our results with those of Dobzhansky and Pavlovsky (1958) is evident. Just as in *D. paulistorum* and *D. willistoni*, the frequency of heterozygotes for certain inversions in the experimental populations of mixed geographic origin fell below the frequency levels in the parental populations. The adaptive superiority of the heterozygotes which carry chromosomes with different gene arrangements is determined by the polygene complexes contained in the inverted sections of the chromosomes. Natural selection tends to act in such a way as to coadapt the gene complexes present in

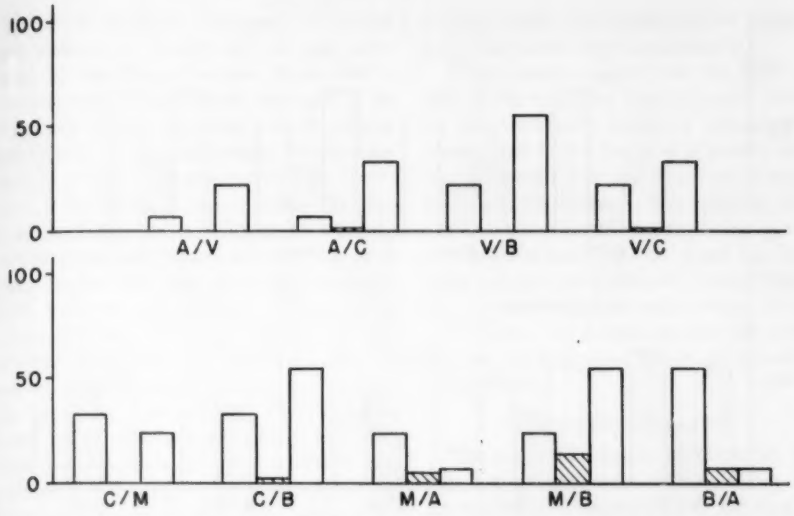

FIG. 1. Frequencies in per cent. (Ordinates) of the heterozygous inverson A + B in the second chromosome in different populations of *D. pavani* and in their hybrids after 10 generations. The white columns indicate the parental populations, the hatched ones represent the hybrid populations. A) *Arrayan*, B) *Bellavista*, C) *Copiapo*, M) *Mendoza*, V) *Vallenar*.

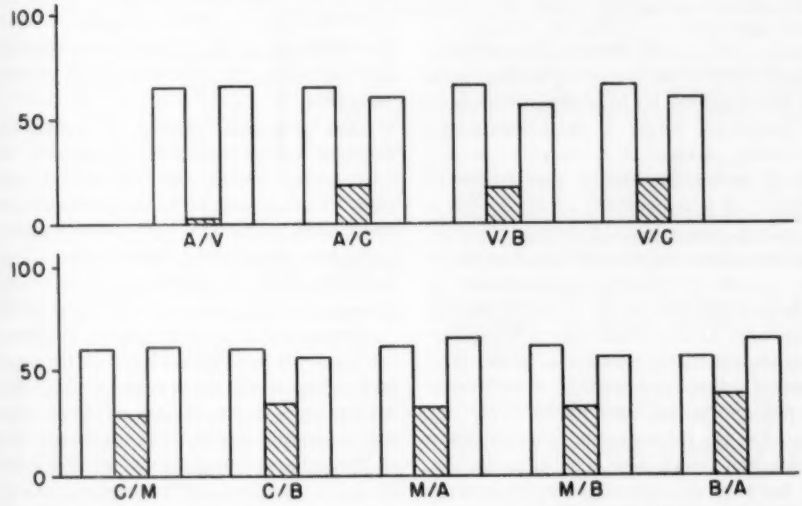

FIG. 2. Frequencies in per cent. (Ordinates) of the heterozygous inversion A + B + C in the IV-R chromosome in different populations of *D. pavani* and in their hybrids after 10 generations. The white columns indicate the parental populations, the hatched ones represent the hybrid populations. A) *Arrayan*, B) *Bellavista*, C) *Copiapo*, M) *Mendoza*, V) *Vallenar*.

each Mendelian population. The role of the inversions is to maintain these balanced gene complexes (*internal balance*) by suppressing recombination. As shown by Dob-

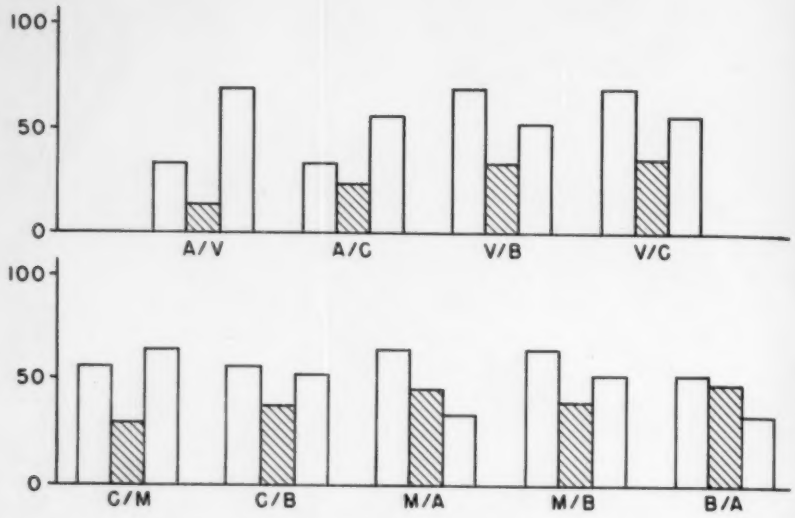

FIG. 3. Frequencies in per cent. (Ordinates) of the heterozygous inversion A + B + C in the IV-L chromosome in different populations of *D. pavani* and in their hybrids after 10 generations. The white columns indicate the parental populations, the hatched ones represent the hybrid populations. A) *Arrayan*, B) *Bellavista*, C) *Copiapo*, M) *Mendoza*, V) *Vallenar*.

zhansky (1957) and Dobzhansky and Pavlovsky (1958), the fitness of homozygotes and heterozygotes for inversions depends on the geographic origin of the chromosomes which they carry.

In *D. pavani*, the drastic decrease of the incidence of heterozygotes for inversions in the mixed populations indicates that the same inversions maintain different balanced gene systems in different populations. In *D. pavani* this finding is of special significance, since in this species no clear qualitative and quantitative variations of the chromosomal polymorphism in different Mendelian populations has been found. This may mean that the chromosomal polymorphism has reached such a high level of perfection, and has been incorporated so permanently into the genetic system of the species, that most changes are likely to be undesirable under normal conditions. An analogous situation may exist in some domestic forms of *Drosophila*, such as *D. funebris*, *D. immigrans*, and others, in which some inversions have wide distribution and frequencies. Nevertheless, an opportunity for evolutionary divergence at the mutational level is preserved.

Each geographic race of *D. pavani* has acquired, under the selective pressures, its own genetic endowment. How far have these changes gone? In many species of *Drosophila* and in other animals and plants, geographic clines in the distribution of certain traits have been observed. The establishment of clines depends in general on the environmental gradients and on the possibilities for gene exchange between the populations into which the species is subdivided. To what extent may it be possible to establish geographic gradients in the distribution of the polygenes maintained by the inversions in *D. pavani*, and in what way can the observed variations be correlated with the dynamics of each particular population? Taking a glance at the table and figures, it can be seen that, in general, the most pronounced breakdowns of the inversion heterozygotes occur in the hybrids between geographically distant populations, such as

Arrayan × *Vallenar*, *Arrayan* × *Copiapo* and *Vallenar* × *Bellavista*. On the other hand, in the crosses between *Bellavista* × *Arrayan* there is hardly any decrease of the frequency of heterozygotes. If the higher breakdown reflects differences in the contents of polygenes maintained by the inversions, it is possible to conclude that the populations of *Arrayan* and *Bellavista* have diverged genetically from one another in a lesser degree than they both have diverged from *Vallenar* and *Copiapo*. This seems reasonable, because the populations of *Bellavista* and *Arrayan* are close, and ecological barriers between them which might prevent the gene flow are lacking. On the other hand, the populations of *Copiapo* and *Vallenar* are very distant from the former, and are isolated in fertile valleys separated by large semidesert and mountain regions. In spite of being relatively near, in point of distance, the populations of *Copiapo* and *Vallenar* show marked genetic differences. By the same criteria, the population of *Mendoza* in Argentina, may be considered genetically nearer to *Arrayan* and *Bellavista* than to the populations of northern Chile. Continuing our speculation, we may conclude that the degree of the breakdown of the heterozygotes for inversions, observed in the crosses between different geographic populations of *D. pavani*, may yield useful information about the genetic relationships of these populations. This may be a useful tool for the establishment of the origin of the different races.

Summary

Crosses were made between geographic races of *D. pavani* from localities in Chile and Argentina. All these populations were polymorphic for the gene arrangements in chromosomes II, IV-R, and IV-L, due to the occurrence of inversions. After ten generations, it was observed that the five parental populations which served as controls have maintained the frequencies of the heterozygotes for the inversions around the same values as found in nature. On the other hand, in the nine populations of mixed geographic origin, the frequencies of heterozygotes decreased very significantly.

These results suggest that the higher fitness of the inversion heterozygotes depends on the internally balanced gene systems maintained in the inverted segments of the chromosomes. Through a process of natural selection, the systems have become different in each Mendelian population. In the interpopulational hybrids these coadapted gene systems are destroyed, owing to crossing over between chomosomes with the same gene orders. As a consequence, the heterozygotes for inversions no longer possess superior fitness.

Acknowledgments

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THERMAL RELATIONS OF FIVE SPECIES OF TROPICAL LIZARDS

RODOLFO RUIBAL
Division of Life Sciences, University of California, Riverside

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The relation of a reptile's body temperature to that of the surrounding environment has been of considerable interest since the work of Cowles and Bogert (1944), and Bogert (1949a). These authors demonstrated that by behavioral methods reptiles were able to maintain their body temperature within a relatively narrow range. Reptiles, in other words, were shown to exhibit a degree of homeostasis in regard to their body temperature. The preferred or eccritic body temperature, was not the same for all the species studied. However, Bogert (*op. cit.*) demonstrated that lizards belonging to the same genus have similar body temperatures, while there may be marked differences between genera.

Virtually all work reported for lizards has been with basking (heliothermic, Cowles, 1940) forms that gain heat from radiant energy. These heliothermic species raise their temperature above that of the surrounding air, and may achieve differences as great as 31° C between their body temperature and that of the surrounding air (Strelnikov, 1944; Pearson, 1954). With few exceptions (Inger, 1959; Bogert, 1949b) the species that have been studied are all temperate region forms, and actually the most intensively studied species have been from semiarid regions.

In this investigation five Cuban species of the neotropical iguanid genus *Anolis* were studied in the field to determine their body temperatures and habitat temperatures. Two of the species were also studied in the laboratory to augment the findings in the field. The five species presented an opportunity to study thermal relations in tropical reptiles. As St. Girons and St. Girons (1956) emphasize, little is known about the thermal relations of tropical reptiles. The tropics represent the zone of the greatest abundance of species and individuals of reptiles. This abundance is in part attributable to the narrow temperature fluctuations of the lowand tropics where the temperature extremes of temperate and subtropical semiarid areas are never encountered.

These five Cuban species represent an extraordinary example of habitat differentiation between closely related species in contiguous habitats. At the localities studied in central Cuba all five species are present, yet each is segregated in a specific ecological niche. As will be described below, the habitats range from the deep shaded portions of the forests, to the margins of the forests where filtered sunlight is present, to the open exposed habitats of the pastures and savannas.

SPECIES AND HABTATS

Five Cuban species of the genus *Anolis* were utilized in this study. Populations of these species in the Provinces of Camaguey and Oriente were studied during July and August, 1957, and 1959. The species studied represent the five most common species of *Anolis* in this part of Cuba. The taxonomy and relationships of some of these species and other aspects of their ecology are discussed in Ruibal and Williams (ms.). All of the species are arboreal and characteristically cling head-down from some vertical perch. All are territorial; the males are restricted in their range and are usually found on the same perch day after day. The species and their habitats are:

A. allogus. This species is a forest-dwelling form found in the shaded portions of the forests. It is characteristic of the deeper parts of the forest where little, if any, sunlight reaches the floor of the forest. The species is restricted to the trunks of small trees and the males are usually perched less than six feet above the ground.

A. lucius. This species is restricted to the

same parts of the forest as *A. allogus* but differing in that it is found on the trunks of large trees (such as the strangler fig, *Ficus*) or on large rock surfaces such as cliffs or cave entrances. The lizards may be stationed from near the ground to a height of over 12 feet.

A. homolechis. This species is restricted to the forest margins, the small clearings, or along paths in the forest. It contrasts to the two previous species in that it is found in areas of moderate sunlight rather than in deep shade. It is usually found on small or large tree trunks below a height of six feet.

A. sagrei. This lizard is a very common form found in open, sunny areas. It is the characteristic lizard of fence posts, gardens, savannas, and exposed coastal vegetation, usually perching less than six feet above the ground.

A. allisoni. This species occurs in the same habitats as *A. sagrei* but differs in that it is usually situated high off the ground (above six feet) on trees, posts, palm trunks, and houses. This species and *sagrei* are the only species found where human activity has extensively altered the natural vegetation.

Most of the data for *homolechis*, *lucius*, and *allogus* were obtained at two forest localities in Camaguey: The Sierra de Cubitas to the north of the City of Camaguey, and at the Finca San Pablo, about 15 kilometers southwest of the City of Camaguey. These are semideciduous forests in which many of the trees lose their leaves late in the dry season for a short period of time. The majority of the data for *allisoni* and *sagrei* were gathered at the Finca Santa Teresa, nine kilometers west of the City of Camaguey where these two species occur in great abundance in the pastures and gardens. *A. sagrei* and *allisoni* are present at the Sierra de Cubitas and at the San Pablo locality, however at these localities an effort was made to sample the other three species that did not occur at Santa Teresa. Small samples (less than 15% of the total sample) of *homolechis* and *allogus* were also made at three forest localities in the Province of Oriente.

With the exception of *homolechis* none of the species demonstrates any evidence of morphological differentiation or subspeciation in the populations studied. In the case of *homolechis* the population from the Sierra de Cubitas is characterized by a yellow dewlap (a large gular appendage diagnostic of the genus) while the San Pablo population has a white dewlap. In the experimental work both forms of *homolechis* were utilized. The field data for these two forms are presented separately.

A. allogus, *homolechis*, and *sagrei* are closely related species. They have the same body size (♂ ♂, snout-vent length averages about 50 mm and weight is approximately 5.5 gm) and occupy the same type of perch (vertical trunks) at the same elevation from the ground (less than six feet). The three species are distinguished in that each occupies a habitat of differing light intensity (insolation) and therefore, the habitats also differ in respect to mean air temperature (see table 2). *Allogus* is in deep shade, *homolechis* in filtered sunlight, and *sagrei* in full sunlight. The other two species, *lucius* and *allisoni*, are not closely related to each other or to the other three species. *A. allisoni* is related to *A. carolinensis* (Ruibal and Williams, 1961, in press) while the only known close relative of *lucius* is another Cuban species, *A. argenteolus*. *A. lucius* share the shaded habitat with *allogus*, but it is a larger species (♂ ♂, snout to vent length averages about 65 mm and weight is approximately 7.5 gm) ecologically separated from *allogus* by its preference for large tree trunks and rock surfaces. *A. allisoni* shares the exposed, open sunny habitats with *sagrei* but is a much larger animal (♂ ♂, snout vent length average about 75 mm and weight is approximately 11 gm) and is ecologically separated from *sagrei* in that it perches at higher levels off the ground.

The habitat segregation of the five species studied is represented diagrammatically in figure 1. All five species occupy distinctive ecological niches. As might be expected

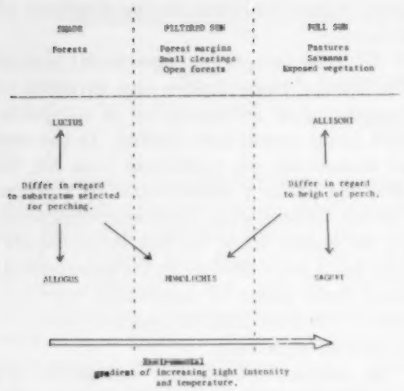

FIG. 1. Diagrammatic representation of the habitat interrelations of the five species studied. The three related species, *allogus*, *homolechis*, and *sagrei*, select perches at approximately the same height (below six feet), but are segregated in that each selects a different portion of the shade-sun gradient. The species that are found in the same temperature-light intensity habitat are segregated in that each selects a different perch.

there is some overlap of the various species. Thus *allogus* and *homolechis* are on occasion found in the same part of the forest and appear to coexist in the narrow areas where the deep shade habitat of *allogus* grades into the filtered sun habitat of *homolechis*. In the few instances observed it appears as though *homolechis* was overlapping the *allogus*-type habitat rather than the converse. Similarly, *homolechis* is found to overlap *sagrei* where their two habitats meet. *A. homolechis* also overlaps with *lucius*, but the two species are, of course, separated by the difference in perching sites. *A. homolechis* possibly overlaps into *allisoni* habitat, although I have never observed individuals of the two species near each other.

FIELD METHODS AND RESULTS

Only adult male specimens were studied. The cloacal temperatures were taken with a Schultheis thermometer (see Bogert, 1949). The animals were captured by means of a nylon thread noose at the end of a five-foot pole. The cloacal temperatures were taken immediately upon capture, the lizards being held by the head, and in the shade while the thermometer reached equilibrium. Air temperatures were recorded at a height of four and one-half feet off the ground, in the shade, and near (a few feet from) the site of capture of the lizard.

Most of the collecting was done between 8:00 A.M. and 4:00 P.M. No diurnal fluctuation in the activity of these lizards was noted. A census of *sagrei* and *allisoni* was taken for four days in the morning (9:00–10:00 A.M.) and in the afternoon (2:00 to 3:00 P.M.) and no consistent difference was found between the morning and afternoon counts. To reduce the possibility of taking the temperature of animals that had emerged from cover and had not yet become

TABLE 1. *The cloacal temperatures of five species of* Anolis. *The balanced sample contains 50% a.m. and 50% p.m. readings. The range is in parentheses under the mean values. All records are for the months of July and August*

Species	A.M.		P.M.		Balanced sample		
	N	Mean	N	Mean	N	Mean	σ_m
A. allogus	74	28.7 (26.2–32.4)	74	29.6 (26.2–33.5)	148	29.2 (26.2–33.5)	.06
A. lucius	50	28.7 (24.8–31.5)	43	29.9 (27.1–32.4)	86	29.3 (24.8–32.4)	.10
A. homolechis	52	31.2 (26.2–36.6)	69	31.9 (29.4–35.0)	104	31.8 (26.2–35.0)	.14
A. sagrei	89	32.2 (27.4–36.4)	125	33.9 (28.3–36.1)	178	33.1 (27.4–36.1)	.22
A. allisoni	61	32.3 (28.2–36.2)	82	33.9 (31.0–37.5)	122	33.0 (28.2–36.6)	.21

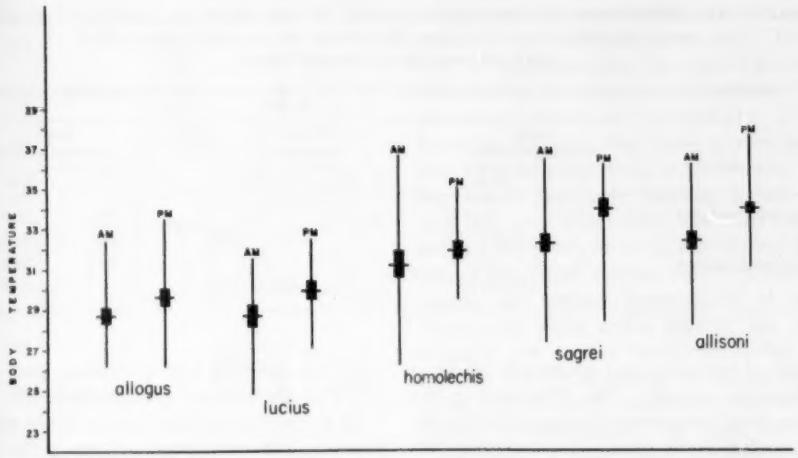

FIG. 2. Comparison of the A.M. and P.M. body temperatures of the five species of *Anolis* studied in the field. The range is represented by the length of the vertical line, the mean by the short horizontal line, and twice the standard error on each side of the mean by the black rectangle. The diurnal shift in body temperature is significant for all of the species.

active, data were recorded only for males at perching sites characteristic of the species. As shown in figure 1 the range of temperatures in the morning samples was greater than that for the afternoon samples in all the species, except *allogus*. However, the lowest body temperatures recorded were not always from the lizards captured earliest in the morning. In *lucius* the lowest temperature recorded was at 11:00 A.M., in *allisoni* at 9:00 A.M., and in *homolechis* at 11:00 A.M. In *sagrei* the lowest temperature recorded (27.4° C at 8:00 A.M.) was the earliest obtained. In *allogus* the lowest temperature recorded, 26.2° C, was obtained a number of times at 10:00 A.M. and also at 1:00 P.M. The wide distribution of low body temperature records throughout the morning (when environmental temperatures are lowest) would suggest that the sample range does represent the "normal activity range" (Cowles and Bogert, *op. cit.*) and that few, if any, records of lizards that had yet to become active were included in the sample. It may also be mentioned that the maximum body temperatures recorded were not all in the afternoon (see table 1).

In figure 2 the total pre-noon and post-noon cloacal temperatures have been separated for each of the five species studied. It is evident that there is a significant difference in the morning mean and range as compared to the afternoon mean and range (see table 1 for the data for all of the species).[1] The shift to higher cloacal temperatures from the morning to the afternoon is correlated with the environmental increase in air temperature between the morning and the afternoon. An increase in the air temperature from morning to afternoon is found in all three habitats (see table 2).

In view of this diurnal shift in body temperatures it is preferable to balance the total samples before comparing one species with another. In table 1 the five species are compared by utilizing samples of equal propor-

[1] In figure 2 twice the standard error of the mean is indicated for all the A.M. and P.M. values and it is evident from this that the differences between the means is significant for four of the species. In the case of *homolechis* there is overlap between the A.M. and P.M. standard errors and therefore it may be questioned whether the difference is significant. A "one-sided" t-test of the A.M. and P.M. means for *homolechis* indicates that the difference of the means is significant at the 5% level (see table 3 for σ_m).

TABLE 2. *Air temperatures of the three habitats studied. All temperatures are with a dry bulb in the shade, at a height of 4.5 feet from the ground. All recordings were made during the months of July and August*

	Habitats					
	Shade (*allogus* and *lucius*)		Filtered sun (*homolechis*)		Sun (*sagrei* and *allisoni*)	
	N	Mean	N	Mean	N	Mean
A.M. temperatures	27	29.6 (26.0–31.8)	17	30.1 (28.2–32.0)	26	30.7 (27.4–32.5)
P.M. temperatures	24	30.4 (27.8–32.4)	11	31.8 (30.0–33.4)	29	33.1 (30.0–35.0)

tions of morning and afternoon readings (balanced sample). The difference in the mean body temperature between the species is correlated with the air temperature of the respective habitats (see table 2). The mean body temperature (MBT) of the two shade dwelling species (*allogus* and *lucius*) are nearly identical as are those of the two sun dwelling species (*sagrei* and *allisoni*). In figure 3 the histograms of the balanced samples illustrate the extent of the differences between the five species.

As mentioned previously, two races of *homolechis*, one with a white dewlap and the other with a yellow dewlap, were studied. The data presented in table 1 refer only to the population with the white dewlap. In table 3 these two races are compared. It is evident from these data that the two races are almost identical in their thermal relations. Both show the morning to afternoon shift in MBT, although the yellow dewlapped population from the Sierra de Cubitas shows a more pronounced shift than the white dewlapped population. However, the temperature ranges obtained for both the morning and afternoon, and the MBT of the balanced sample are similar.

In figure 4 isothermal plots of the air temperature and cloacal temperature of the lizards are compared. Sample sizes in these plots are smaller than for the data in table 1, because the environmental air temperature was not taken for every lizard recorded. The data on the yellow and white dewlap races of *homolechis* are combined in the plot in figure 4. In the case of *homolechis*, *sagrei*, and *allisoni* the plots are as would be anticipated for heliothermic species. That is, body temperatures are generally above the air temperatures, as expected in an animal that absorbs radiant energy. In contrast, *allogus* and *lucius* present a new and unique situation in that the plots show that the body temperatures of these animals are generally below that of the air. These shade-dwelling forms inhabit an environment low in radiant energy as compared to that of the heliothermic species. These animals perch on tree trunks or on rocks that are usually moist (certainly in the wet summer), and consequently are probably below

TABLE 3. *Comparison of the mean body temperatures of two geographic races of* A. homolechis. *The range is in parentheses below the mean*

	A.M.			P.M.			Balanced sample		
	N	Mean	σ_m	N	Mean	σ_m	N	Mean	σ_m
White dewlap race	52	31.2 (26.2–36.6)	.30	69	31.9 (29.4–35.0)	.21	104	31.8 (26.2–35.0)	.14
Yellow dewlap race	24	30.8 (26.8–36.2)	.55	36	32.5 (29.8–35.4)	.25	48	31.7 (26.8–35.4)	.37

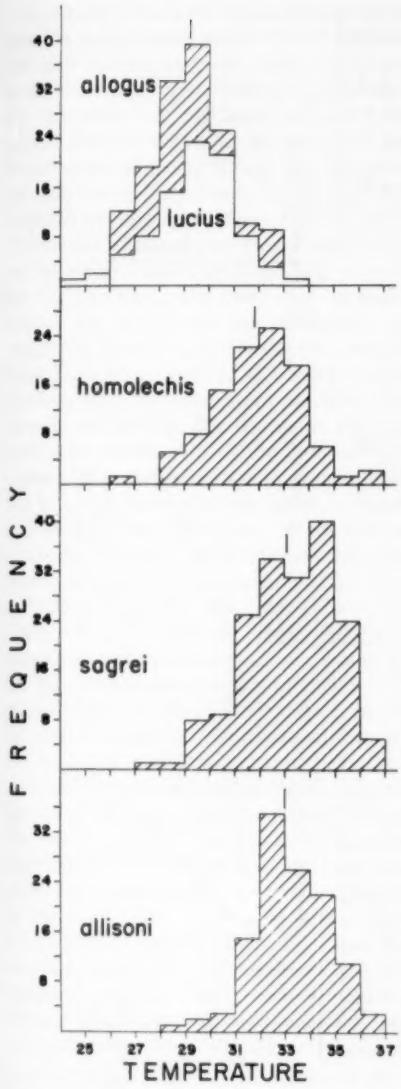

FIG. 3. Histograms of the balanced samples of the five species. The range in cloacal temperatures for each species is believed to represent the normal activity range. The small vertical line above each histogram marks the mean, which approximates the mode in all cases.

the air temperature. Since thermometers provide only an inaccurate measure of the surface temperature of solids, substrate temperatures were not made in the field. However, it is apparent that the exposed perches of the heliothermic species can be heated by the sun to above air temperature. It is therefore plausible that these species gain heat by conduction from the substrate. In the case of the shade dwelling species no such heat gain is possible. The deep shade at the lower levels of tropical broadleaf forests is devoid of radiant heat capable of raising the surface temperature of tree trunks and rocks above that of the air.[2] Actually due to the rapid conduction of heat by solids the perches of *allogus* and *lucius* are probably consistently below the diurnal environmental air temperature. Under these circumstances the only source of heat for the non-heliothermic species (other than an endothermic source) is the air. The transfer of heat by conduction from air is slow and consequently in a perching immobile animal, heat lost by evaporation (respiratory) and conduction to the substratum result in a body temperature below that of the air. This interpretation is supported by the work of Lueth (1941) who demonstrated that in the absence of radiant heat snakes have body temperatures below the air temperatures.

EXPERIMENTAL METHODS AND RESULTS

Live lizards brought back to the laboratory in Riverside, California, in September of 1959, were maintained in terraria of various sizes. Some of the terraria were kept in a greenhouse having a temperature that fluctuated between 22° C and 30° C, while the majority of the terraria were kept along windows in the laboratory and were exposed to temperature fluctuations that ranged from approximately 19° C to 31° C. The animals were fed mealworms (*Tenebrio* larvae) and waxworms (*Galleria* larvae). They were periodically given a multivitamin preparation in water and occasionally exposed to ultraviolet radiation. All the ani-

[2] Geiger (1957) cites measurements of illumination in tropical forests which indicate that at elevations less than 2 meters from the forest floor less than 1% of the outside illumination is present.

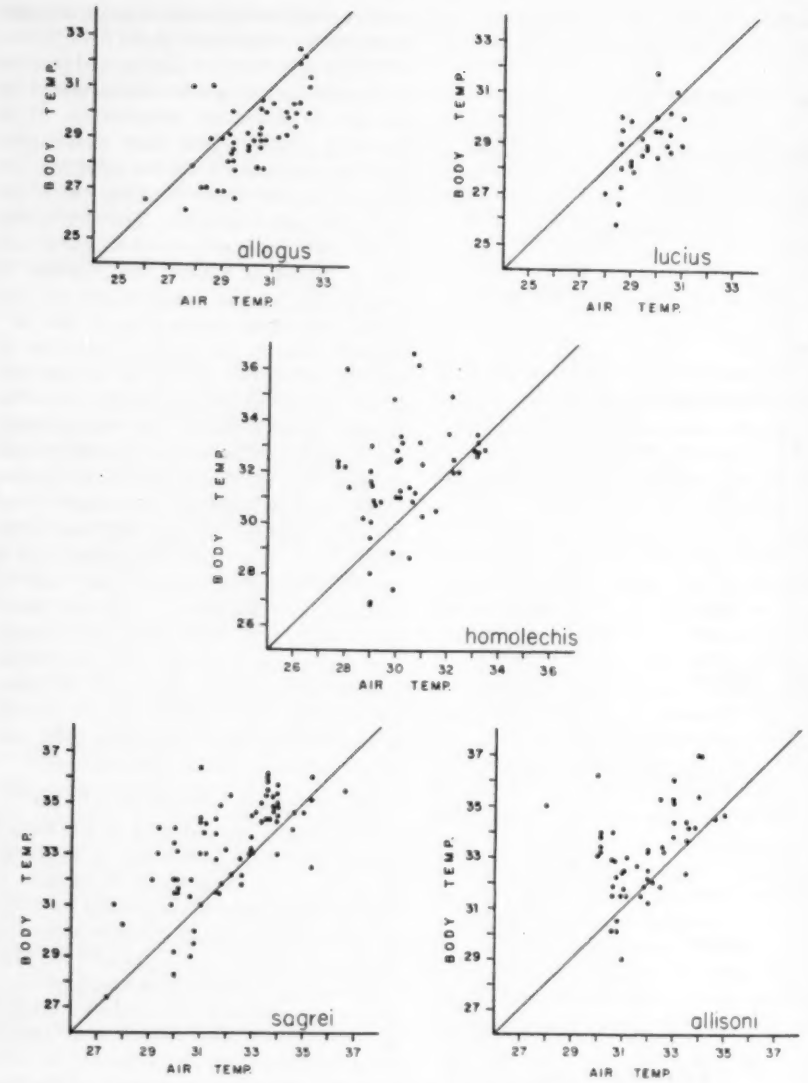

FIG. 4. Isothermal plots of the body temperatures and environmental temperatures of the five species of *Anolis* studied. In *allogus* and *lucius*, the two shade dwelling species, the body temperatures were predominantly below the air temperatures. In contrast the three species that bask (*homolechis*, *sagrei*, and *allisoni*) are characterized by having the body temperature above the air temperature.

mals appeared to be healthy and vigorous when utilized in the laboratory experiments. The animals had been in captivity for four months when tested for temperature sensitivity. Only males were used in the experiments.

A simple apparatus was constructed to test the temperature sensitivity of *homolechis* and *allogus*. A glass battery jar 24 cm in diameter and 30 cm in height was used as the container. A 250 watt infrared bulb placed directly above the jar served as the heat source. A moist sponge was placed at the bottom of the jar and the jar was surrounded by wood panels about 45 cm high. The distance from the surface of the sponge to the surface of the infrared bulb was 57 cm (22.5 inches). The purpose of the moist sponge was to prevent the substratum on which the lizard was to stand (the sponge) from heating up rapidly. If a moist sponge was not used, the substratum would rapidly become so hot that the lizards would curl their toes, move, and lift the feet avoiding contact with the substratum. During tests the infrared lamp was turned on, a lizard was dropped onto the sponge at the bottom of the jar, and the test was terminated (the lizard removed) when the animal made a definite movement toward the side of the container. The cloacal temperature was taken just before the animal was placed in the jar and was also taken on removing the animal from the jar. The time spent in the jar was also recorded. In this manner a record of the rate of increase in the body temperature of the lizard was made as well as a record of the temperature tolerated before the lizard attempted to escape. It must be emphasized that this type of test was possible due to the peculiarity of these lizards to "freeze" when introduced into a new environment. Characteristically these lizards are territorial and aggressive. When removed from their home ground (the terraria in which they had been living for four months) and placed into a new container, however, they remain motionless for prolonged periods of time. Control tests of the apparatus and of the lizards were done without the infrared lamp. Under these circumstances the lizards remain motionless for periods in excess of ten minutes. In contrast during the tests when exposed to heat from the infrared lamp 90% of the animals moved in less than five minutes. The test was thus simply one of placing the lizard in a situation where it would normally remain motionless and then causing a rise in the body temperature and recording the temperature when the urge to escape the heat overcame the tendency to stay motionless.

TABLE 4. *Means and range of body temperatures (°C) at which movement is initiated by ♂ specimens of* A. allogus *and* A. homolechis *in the test apparatus. The range is in parentheses below the mean values*

Species	Number of tests	Mean (range)	σ	σ_M
Allogus	37	32.4 (29.5–35.0)	1.67	.27
Homolechis	42	34.7 (29.0–38.8)	2.24	.35

In order to reduce the possibility of conditioning the animals no lizard was tested more than once every five days. Records were kept of individual animals and all were run as controls at least once. Tests that ran for less than one and one-half minutes are excluded from the data presented here. In about 16% of the tests the animals either failed to remain motionless, initiated movements in less than one and one-half minutes, or moved because of some outside disturbance; such tests were not included in the calculations.

The initial body temperature of the lizards (before being placed in the test jar) ranged from 23 to 28° C. A total of 17 male specimens of *homolechis* and 12 male specimens of *allogus* were utilized in the experiments.

The results of these experiments are tabulated in table 4. It is immediately evident that *allogus* and *homolechis* differ in regard to the temperature that they will tolerate before initiating movement in the experimental jar. The mean temperature for *allogus* is 31.8° while *homolechis*, as would have been expected from the field data, tolerates a higher mean temperature, 34.6° before moving.

The rate at which the lizard gains heat under the experimental conditions can be estimated. Dividing the increase in heat (°C) by the duration (minutes) of the test

TABLE 5. *Means and range of body temperatures (°C) at which panting is initiated by* A. allogus *and* A. homolechis. *The range is in parentheses below the mean value*

Species	Number of tests	Mean (range)	σ	σ_M
Allogus	42	30.3 (28.5–32.8)	1.28	.20
Homolechis	40	36.2 (32.8–39.4)	1.72	.27

provides a method of comparing the two species. This calculation assumes that the heat gain was uniform throughout the experiment, and of course this was probably not the case. Most specimens of *allogus* started panting during the tests and thus presumably increased heat dissipation. Furthermore, all lizards were not exposed to the same amount of radiant heat since the infrared lamp did not project heat uniformly over the sponge on which the lizards were standing. Despite these shortcomings in the tests the rate was calculated and found to be approximately 2° C/minute for each species.

A further test of the temperature sensitivity of these two species was conducted by introducing the animal into the same test apparatus as described above, but in this instance the cloacal temperature of the animal was taken when it initiated panting. The initiation of panting was defined as when the lizard opened its mouth while ventilating the lungs. The results of these tests are tabulated in table 5. It is apparent that the temperature sensitivity difference between *allogus* and *homolechis* is even more pronounced in this test than in the previous test of initiation of movement. *A. allogus* increases heat dissipation by panting at an average temperature of 30° C, this being only 1° above the average body temperature (29.2° C) determined in the field. In contrast *homolechis* begins to pant at an average body temperature of 36° C, and thus is not increasing its heat dissipation until the body temperature is about 4° C above the MBT.

The sensitivity of *allogus* to high temperatures in the laboratory experiments confirmed an observation made in the field when specimens of *allogus* were brought from their forest habitat and kept in a large cage at the Finca Santa Teresa. The cage was always on a porch in the shade on the east side of a house. Bowls of water for drinking were kept in the cage for the lizards and it was found that every afternoon, when the air temperatures had risen, the *allogus* were to be found immersed in the water of the drinking bowls. This behavior was predictable and in some cases all but the head of the lizard remained submerged below the surface of the water. Whether the animals make use of this behavioral trait in nature is not known.

What role acclimatization may have in the experimental differences between *allogus* and *homolechis* is difficult to determine. Certainly the four months in captivity exposed the two species to a more equal temperature environment than they occupy in nature. Nevertheless, even in a terrarium lizards have access to a variety of temperatures. On warm days the specimens of *allogus* would be pressed against the cool, moist sand in the shade at the bottom of the terraria while the *homolechis* would be on perches exposed to radiant heat. Therefore, although the two species were kept at what might be considered equal conditions they, nevertheless, found different preferred temperatures.

DISCUSSION

Habitats. The field data demonstrate that three separate temperature habitats are occupied by the five species studied. It further indicates that species occupying the same temperature habitat are isolated by a difference in perch selection. The situation described for these five sympatric species conforms to Gause's principle. In this study only two ecological factors (temperature and perch) have been mentioned. However, other differences in habits and behavior further emphasize the distinctness of the ecological niche that each species occupies. Thus, the females of *lucius* have communal egg laying sites in holes and crevasses in the rocks or in hollow tree trunks. As far as

known the other species lay eggs in humus or rotting wood, but it must be emphasized that little is known concerning their reproductive behavior. Three species, *allogus*, *homolechis*, and *sagrei* often forage on the ground in contrast to the other species. When frightened and fleeing *allisoni* and *lucius* climb to the higher levels of the tree or rock upon which they perch. In contrast *allogus*, *homolechis*, and *sagrei* escape by running down from their perch. These aspects of their behavior have yet to be studied in detail.

Currently *sagrei* and *allisoni* are the most abundant species of lizard in central Cuba. This appears to be a recent phenomenon associated with the destruction of the forests and the introduction of agriculture. Previous to modern man's activities *allisoni* and *sagrei* were probably restricted to the natural open associations such as the savannas and coastal areas from which they invaded the areas that man cleared.

The question of whether the various species select their habitat on the basis of temperature, light intensity, or other factors is yet to be answered. Experimental results demonstrating the existence of pronounced differences in the temperature sensitivity of *allogus* and *homolechis* support the hypothesis that temperature preference influences the choice of habitat. Certainly the sensitivity of *allogus* to high temperature would cause this species to avoid the habitats of *homolechis* and *sagrei*.

Relatively little overlap of the various ecological niches is observed in the field. Each species seems to recognize an invisible boundary that separates it from the contiguous species. Temperature preference alone may not account for this separation. The fact that the species are sharply segregated reflects the effectiveness of natural selection in reducing interspecific contacts. Selection has probably operated on many aspects of the lizard's ecology and behavior and therefore habitat selection is not attributable to any single element in the environment. This study reveals that habitat selection in *Anolis* depends to some degree upon perch preference and temperature preference.

The interrelationship of these species is further complicated in that a number of other species of *Anolis* are found in the same habitats. In the shaded portions of the forest a third species, *alutaceous*, perches on thin twigs and grass. In open sunny habitats three other species, *angusticeps*, *porcatus*, and *equestris*, are found together with *sagrei* and *allisoni*. Three other species, *loysiana*, *argillaceous*, and *isolepis*, are also found in the forest or margins of the forest, but their rareness precluded a precise determination of their habitat. The ecological niche each of these species occupies has yet to be determined. The abundance of species of Cuban *Anolis* makes these lizards particularly suitable for the study of interspecific relationships. The situation in many respects is comparable to that described for the Galapagos finches by Lack (1947) and may, with future study, help to clarify our concept of interspecific competition.

Temperature. The results of this study differ from the results obtained by Bogert (1949a, and 1949b) in his investigation of the body temperatures of various species of *Sceloporus* and *Cnemidophorus* of the United States and Mexico. The difference between morning and afternoon mean body temperatures recorded for the species of *Anolis* is presumed not to occur in *Sceloporus*. The existence of higher means in the afternoon implies that when comparing one species with another, the possibility of a diurnal shift in the MBT must be considered and the sample distribution checked to avoid introducing error. If *Sceloporus* and *Cnemidophorus* lack a diurnal shift in the MBT it signifies that these lizards are able to exert greater control in regard to their body temperature than the tropical *Anolis*. However, unpublished data obtained by T. L. Rodgers on *Sceloporus graciosus* and *S. occidentalis* in California indicate that a diurnal shift comparable to that described here for *Anolis* occurs in these two species.

In contrast to the situation in *Sceloporus* where closely related species have the same

MBT (Bogert, 1959), the MBT of the three closely related Cuban species (*allogus*, *homolechis*, and *sagrei*) differ significantly. These species resemble each other only in perch selection. One can conclude from this that in the evolution of the various species of Cuban anoles perch preference has been conservative within groups of related species while the habitats selected (and consequently temperature preferences) have diverged.

The more distantly related species that share a common habitat (*lucius* and *allogus* in the shade, and *sagrei* and *allisoni* in the sun) have nearly identical MBT. Therefore, the members of each of these pairs although occupying spatially different parts of the habitat (i.e., *lucius* on the rocks and large tree trunks while *allogus* is on the small trees) apparently occupy identical thermal environments.

Furthermore, the species of *Anolis* differ from the North American species in their relation of the body temperature to the air temperature. The diurnal shift in the MBT of the various species is correlated with the diurnal shift in the air temperature. Consequently, the isothermal plots (figure 4) demonstrate that as air temperatures rise body temperatures also rise. This correlation is evident for the non-basking species as well as for the heliothermic species. Furthermore, *lucius* and *allogus* are unique in that these species demonstrate body temperatures that are consistently below the air temperatures. These shade dwelling species exemplify reptiles in which behavioral mechanisms probably play a small role in the maintenance of body temperatures. These species are devoid of a source of radiant heat to raise the body temperature and are passively dependent upon the environmental air as a source of heat. They possess behavioral mechanisms for reducing the body temperature (panting and immersion in water) but lack mechanisms to raise the body temperature.

It has yet to be determined whether *allogus* and *lucius* are facultative or obligatory non-heliotherms. In most of the areas inhabited by these species no sunlight is available for basking. However, some of the Cuban forests are semideciduous, losing their leaves for a short period of time at the end of the dry season (March–April). Under these circumstances sunlight is present near the forest floor and these species may consequently bask during this time. In the laboratory tests *allogus* demonstrates a high sensitivity to radiant energy, and it is therefore also possible that it is physiologically an obligatory non-heliotherm.

The only published example of a reptile showing a thermal relationship similar to *allogus* and *lucius* is that of *Sphenomorphus sabanus* studied by Inger (1959). This Bornean skink is forest dwelling and non-basking. Inger obtained sixteen records of the body temperature of this species and demonstrated that the body temperature averaged only 0.6° C above the air temperature. The lizards were shot before the body temperature was recorded and Inger suggests that the temperature may have been raised by the shot that penetrated the lizards. Furthermore skinks are not stationary, perching lizards like the species of *Anolis*, but rather are active moving animals and consequently are producing heat from muscular activity. This probably would be sufficient to raise their body temperature equal to that of the air. In any case, *S. sabanus* represents a non-heliothermic species, and together with *A. allogus* and *A. lucius* indicates that non-heliothermy may be widespread in tropical reptiles. It appears that the evolution of non-basking reptiles is possible in the tropics where the environmental air temperatures remain relatively constant and high. Regions of low air temperature (high mountains and temperate areas) represent a barrier to invasion and occupancy by shade dwelling species. The invasion of the more temperate climatic regions is more feasible for heliothermic reptiles. A peculiarity of this phenomenon is that the tropical reptiles adapted to high temperatures are preadapted to invade colder regions. The shade dwelling tropical reptiles are adapted to lower temperatures than their sun bask-

ing relatives, yet this same adaptation probably hinders their invading non-tropical areas.

Of the lizards that inhabit the United States, only nocturnal and subterranean species are not directly dependent upon solar radiation for the maintenance of their body temperature and are therefore comparable to the shade dwelling tropical species. The native nocturnal species (*Coleonyx*, *Phyllodactylus*, *Xantusia*, and *Heloderma*) are limited to areas of high insolation (southwestern United States) where the air and ground retain relatively high temperatures during the night. The introduced nocturnal species (*Sphaerodactylus*, *Hemidactylus*, and *Gonatodes*) are restricted to Florida, an essentially tropical region. The subterranean species (*Anniella*, *Rhineura*, and *Neoseps*) inhabit environments that simulate the tropics in respect to the narrow temperature fluctuations that characterize their subsurface habitat. They are further restricted to areas of relatively high temperatures (California and Florida). One subterranean form, *Ophisaurus*, is in contrast wide ranging (extending from the Gulf coast to Wisconsin). However, this species is heliothermic and is known to bask (Fitch, 1956). One North American diurnal species that might resemble the shade dwelling *Anolis* and *Sphenomorphus* is the skink *Lygosoma laterale*. Fitch (*op. cit.*) notes that this species is most common in the shaded portions of the forest in Kansas. If this species is non-heliothermic, it would be expected to have a lower normal activity range than the other diurnal lizards. Fitch has obtained a few (sixteen) body temperature determinations of *Lygosoma* and these indicate a preferred range of 27°–31° C, lower than any recorded for a North American diurnal lizard. However, these determinations were many degrees above the air temperature at the time of capture and indicate that the lizards had probably been basking previous to capture.

Charles Bogert of the American Museum of Natural History has pointed out to me that the species of *Gerrhonotus* in the western United States probably represent examples of non-heliotherms that are adapted to temperate climates. This certainly seems to be the case for *G. coeruleus* since this species ranges from California to British Columbia and is usually associated with cool and shady coniferous forests. Most of the gerrhonotine lizards from tropical Mexico and Central America are characteristically found in forests at high altitudes. The entire group may well represent specialized low temperature adapted lizards that have successfully occupied non-heliotherm niches in cool forests.

The information so far gained concerning the thermal relations of lizards permits the recognition of the following two categories:

a) heliothermic species that bask in the sun, absorb radiant heat, and are characterized by having high MBT (above 31° C).

b) non-heliothermic species that do not bask and have low MBT (below 31° C). These non-heliothermic (or thigmothermic as suggested by Cowles, 1940) species may be arboreal or terrestrial shade dwelling species deriving their heat from the air; nocturnal species obtaining heat by conduction from the substratum or the adjacent air; burrowing species that derive their heat by conduction from the surrounding soil.

Most species of non-heliothermic lizards will possibly prove to be facultative non-heliotherms. They will be tolerant of relatively low temperatures (around 25° C) but capable of basking when the air temperatures are lower than the preferred body temperature. However, it must be made clear that for basking to be possible the habitat of a facultative non-heliotherm must provide basking sites. Tropical species such as *Anolis allogus* inhabit forests where no basking sites are available. A lizard in temperature regions adapted to a habitat comparable to that of *A. allogus* would require the added adaptation of a tolerance to very low MBT (below 20° C).

All of the data obtained concerning the thermal relations of heliothermic reptiles (see St. Girons and St. Girons, 1956, for references) demonstrate that heliothermic

lizards have higher body temperatures than heliothermic snakes. This has proved true even for lizards and snakes found in the same areas (Fitch, *op. cit.*, and St. Girons and St. Girons, *op. cit.*). The mean body temperatures determined for diurnal heliothermic snakes (*Thamnophis*, *Elaphe*, *Agkistrodon*, *Coluber*, etc.) are all below 32° C and comparable to those obtained for the shade dwelling species of *Anolis*. This is a curious fact explicable as a consequence of the evolutionary history of snakes. For various anatomical reasons it has been assumed that snakes evolved from ancestral burrowing lizards, and consequently diurnal snakes are secondarily diurnal. Though we have little information concerning the MBT of fossorial lizards, it appears obvious that they have low body temperatures comparable to those of shade dwelling species. In view of this it seems plausible (as Cowles, *op. cit.*, suggested in regard to the low thermal tolerance of snakes) that the low preferred temperatures of heliothermic snakes is a reflection of their evolution from non-heliothermic fossorial lizards.

Acknowledgments

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Summary and Conclusions

1. Five arboreal Cuban species of the lizard genus *Anolis* were found to occupy three contiguous thermal habitats: shade, filtered sun, and full sun.

2. The three closely related species (*sagrei*, *homolechis*, and *allogus*) have different temperature preferences but similar perching preference. The species occupying the same thermal habitat are not closely related and differ in perching habits.

3. It is concluded that in the evolution of the Cuban species of *Anolis* perching habits have been conservative within related species, while the thermal habitat selected (or temperature preference) has diverged.

4. Two of the species, *sagrei* and *allisoni*, are basking forms found in the open cultivated areas and natural clearings and savannas. These two species have a mean body temperature (MBT) of approximately 33° C and are true heliothermic reptiles that maintain their body temperatures above that of the air.

5. One of the species, *homolechis*, inhabits the filtered sun habitat found at the edges of the forests and the small clearings in the forests. This is a heliothermic species with a MBT of 31.8° C.

6. The two other species, *allogus* and *lucius*, are shade dwellers found in the denser portions of the forest. The MBT of these two species is relatively low, 29° C. These species are unique in that body temperatures are usually below those of the air of their habitat. These species, therefore, are not heliothermic.

7. The fact that *allogus* and *lucius* have body temperatures below that of the air is attributed to the absence of radiant heat in the shaded portions of the forest, and to the probable loss of heat by these lizards by respiration and to the substratum.

8. All five species studied demonstrate a significant upward shift in the MBT between the morning and the afternoon. This diurnal shift is correlated with the rise in the environmental air temperature. The diurnal shift in the MBT is presumed to be related to the rising environmental tempera-

ture. The higher afternoon MBT reflects the fact that by the afternoon most of the animals are operating near the upper end of their normal activity range.

9. Laboratory experiments demonstrate that *allogus and homolechis* differ in their temperature sensitivity. Under the experimental conditions *allogus* begins to pant at a mean body temperature of 30° C and to initiate escape movements at 32.4° C. In contrast, *homolechis* pants at 36° C and moves to escape at 34.7° C.

10. The extreme difference in the temperature sensitivity of these two species indicates that habitat selection depends in part, upon the thermal sensitivity of the various species.

11. It is suggested that non-heliothermic lizards are passively dependent upon the environmental air temperature and consequently behavioral mechanisms play a small role in thermal regulation. In contrast the tropical heliothermic species, because of their basking habit, are viewed as preadapted to invade temperate areas.

12. Following Cowles' (1940) original suggestion, lizards are divided into two categories:

Heliotherms, or sunbasking lizards, that gain heat by absorbing radiant energy and have high body temperatures.

Non-heliotherms, or *thigmotherms*, that gain heat by conduction from the surrounding environment (air, soil, etc.) and demonstrate low body temperatures.

13. The diurnal non-heliothermic lizards may be facultative non-heliotherms and utilize basking when air temperatures are low. However, it is also suggested that some of these forms may prove to be physiologically obligatory non-heliotherms.

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NOTES AND COMMENTS

A BASIC WORK ON EVOLUTIONARY THEORY

GEORGE GAYLORD SIMPSON
Museum of Comparative Zoology, Harvard University

The modern synthetic theory of evolution is now very extensively documented in thousands of papers and scores of books. Its main foundation and basic exposition may, however, be seen in a dozen books or so, published from 1930 to about 1955. Prominent among them is Rensch's *Neuere Probleme der Abstammungslehre*, subtitled *Die transspezifische Evolution*, originally published in 1947. Because of war conditions, Rensch was unaware until the last minutes of proof correction that several works, each an amazingly close parallel of parts of his, had been published some three to five years earlier in England and the United States. He welcomed this coincidence as strong evidence of a growing consensus on evolutionary theory and of the firmness of its major conclusions. The renewal of communication enabled him to knit the synthesis still more closely and more knowingly in a heavily revised second edition issued in Germany in 1954. An English translation, which is also a further revision, is now made available under the title of *Evolution above the Species Level*.[1]

In preparing a text for translation the author evidently went through the whole book carefully again. He did no important rewriting, but clarified various points, inserted brief mention of some more recent work, and slightly abridged a few passages. It is thus true both that "only a few alterations and additions have been made," as the author says, and that this is "truly a new edition," as the publishers claim. The translation is not entirely free of shortcomings. Occasionally, as when "in den verschiedensten geologischen Epochen" is translated "in some geological epochs," these are serious misinterpretations. More often, as when "Kladogenese" is half-anglicized as "kladogenesis" instead of the fully anglicized "cladogenesis," they are only trifling annoyances. The task of translation is more than linguistic, as may be exemplified by the fact that although "Silurian" is an etymologically correct translation of "Silur" the latter word, as used by Rensch, includes both the Ordovician and the Silurian of English-speaking geologists. Failure to take that consistently into account is seriously confusing. Other examples, such as "ground hogs" for "Erdferkeln," which looks so right and is so ludicrously wrong, are more amusing than serious. This was, however, an exceptionally difficult book to translate and in general the English does clearly convey the thought of the original.

[1] 419 pages, 113 figures, 21 tables. Columbia University Press, New York, 1960. $10.00.

The book begins with brief consideration of the causative factors of infraspecific evolution, listed as mutation, recombination and gene flow (including hybridization), fluctuation of population size, isolation, and selection. The main theme of the work is argument that these same factors are also sufficient to account for the known phenomena of supra- or transspecific evolution. The opposing views most persistently cited are those of a number of Germanic paleontologists, including Beurlen, Dacqué, Schindewolf, Von Huene, and Wedekind, who sometimes seem to be accepted as the authentic, but mistaken, voice of paleontology. It is natural that Rensch emphasized the paleontological studies most accessible to him and most influential in his own milieu. A revision intended for a non-German audience might, however, have given more prominence to the fact that many paleontologists elsewhere are of his opinion (or that he is of theirs!) and that they have devoted much attention to refuting the views he also opposes. One American paleontologist, Osborn, is in the group adversely cited, but Osborn died before the synthetic theory was developed, and his own theoretical views had no other paleontological adherents even in his lifetime.

In pursuance of the theme, it is first demonstrated that no sharp line can be drawn between "race" (subspecies) and species formation. The "undirected," or opportunistic, and "directed," or apparently orthogenetic, aspects of evolution are then contrasted and it is concluded that natural selection can account for the latter aspect, at least. Briefer discussion of rates of evolution leads to the conclusion that rates, also, are primarily influenced by selection. The heart of the book and slightly over half its text length are in chapter 6, on "The Rules of Kladogenesis (Phylogenetic Branching)." In fact most of this section relates to phenomena that commonly occur within branching phylogenies and that may be involved in the divergence of lineages but that are not more directly related to cladogenesis *per se*, defined as the actual process of branching or splitting. The major topics are: explosive radiation; specialization, stressing irreversibility and allometric growth and also, perhaps oddly, including parallel evolution and orthogenesis; overspecialization, degeneration, and extinction; phylogenetic effects of genetic modifications in ontogeny; and the origin of new structural types and organs.

A chapter on anagenesis (Rensch's term, recently adopted with a slightly different definition by Huxley) deals with general tendencies for evolving

groups of organisms to progress through stages of increasing complexity, rationalization (in a sense rather mechanical than psychological), plasticity, potentiality for further improvement, and autonomy. The phenomena treated are those that gave rise to the old idea of a ladder of nature, but Rensch is, of course, clear that the progressive tendencies are neither uniform nor universal and that when they do occur they are explicable by natural selection. A short chapter called "The Evolution of Life" is devoted to the origin of life, which is concluded to have occurred from the inorganic by natural, material processes. A summarizing chapter then closes the whole argument with the conclusion that "There is no reason to assume noncausal or autonomous processes in evolution."

It is, in my opinion, unfortunate that that is not the last chapter of the book, which goes on for 36 pages on the "Evolution of the Phenomena of Consciousness." Rensch says, ". . . I have not omitted this chapter because the majority of the readers of the German edition . . . considered it essential and stimulating," which seems to imply that some readers nevertheless did suggest its omission. Even now that it has been somewhat clarified and put into English, the text here is exceedingly difficult for anyone outside the atmosphere of German philosophy. Such of it as is truly relevant to the book's theme could have been, and indeed in part has been, expressed more simply where pertinent in previous chapters. Most of it, however, seems to me irrelevant or at times even contradictory in this particular context.

Rensch's extensive discussions and very rich examples range over the whole field of zoology. It is inevitable that a specialist in any one part of that enormous subject will find numerous minor mistakes. For example, in my own field the following are just some of the errors encountered within a few pages: *Hapalops* is not an armadillo; *Pyrotherium* is neither a notoungulate nor of Miocene age; *Megalocnus* is not a giant for its group but distinctly below average size (the translation omits the rather indefinite qualification "bärengrosse" of the original text); *Aepyornis* is not an ostrich; *Hoplophoneus* does not occur in the Eocene; the Pterosauria are not marine reptiles. It should be stressed, however, that I did not note any point where such errors entirely invalidated the conclusions drawn.

In spite of some drawbacks, which have in honesty been mentioned but not, I hope, overemphasized, this is one of the really important and essential works in its field. It must be studied by everyone who aspires to any competence in modern evolutionary theory. We should all be grateful that it is now available in English.

BOOKS RECEIVED

Notices will be given under this heading of books of evolutionary interest sent to the Editors. Appearance of a title in this section will not preclude a fuller review in a later issue of the journal.

Tsitsin, N. V. (ed. in chief). 1960. Distant Hybridization of Plants and Animals (title translated). 597 pp. illus. 26.60 roubles. U.S.S.R. Acad. of Sci. Moscow.

——. 1960. Distant Hybridization of Plants (title translated). 435 pp. illus. 15.40 roubles. State Agric. Publ. Moscow.

Two volumes in Russian of the proceedings of a conference on interspecific hybridization held in Moscow in 1958, containing over 80 reviews and articles describing original experiments on hybrids of cereals, vegetable crops, fruit and forest trees, large domestic and wild animals, and fish.

Gardner, Eldon J. 1960. Principles of Genetics. VII + 366 pp. illus. $7.50. Wiley. New York. A textbook of genetics intended for a first college course in the subject.

Mayfield, H. 1960. The Kirtland's Warbler. XV + 242 pp. illus. $6.00. Cranbrook Institute of Science. Bloomfield Hills, Michigan. A monographic treatment of the life history of an exceedingly interesting relict species of bird.

Howells, William. 1959. Mankind in the Making. 382 pp. illus. $4.95. Doubleday. Garden City, N. Y. An illustrated account of human evolution on a nontechnical level, bringing up to date the author's well-known "Mankind So Far."

Tax, Sol, and Charles Callender (eds.). 1960. Evolution after Darwin. Vol. 3. Issues in Evolution. VIII + 310 pp. illus. $7.50. University of Chicago Press. Chicago. The concluding volume of the *Evolution after Darwin* trilogy (reviewed in EVOLUTION, **14**: 533) contains three papers dealing with evolution and religion, transcripts of two television programs dealing with the Darwinian celebration, an account of its organization, Julian Huxley's convocation address, a general index to the whole series, and, above all, edited transcripts of panel discussions which were the focal point of the commemoration. The contributors to the first two volumes participated in five of these, respectively entitled: the origin of life; the evolution of life; man as an organism; the evolution of mind; social and cultural evolution. The record of the discussions is complementary to the formal papers and contains a great deal of additional factual and speculative material. It provides a delightfully informal and exceedingly important documentation of the state of evolutionary thought at the end of Darwinism's first century.

Dobzhansky, Th. 1960. The Biological Basis of Human Freedom. VI + 139 pp. $1.25. Columbia University Press. N. Y. A paperback reprint of the earlier edition of Dobzhansky's 1954 lecture series at the University of Virginia.

Harper Torchbooks. The Science Library. 1960. Further paperback reprints by Harper, New York, of biological monographs. The dates given in parentheses are of the original publications:

Dowdeswell, W. H. (1955). The Mechanism of Evolution. IX + 115 pp. 25 figs. $0.95.

Morton, J. E. (1958). Molluscs. 232 pp. 23 figs. $1.40.

Sheppard, P. M. (1958). Natural Selection and Heredity. 209 pp. 8 figs. $1.35.

ANNOUNCEMENTS

The American Society of Ichthyologists and Herpetologists announces the preparation of a new edition of the Society-sponsored *Checklist of American Amphibians and Reptiles*. The new checklist will have a completely revised format with greater detail than any previous edition, will be a loose-leaf publication, and will be authored by many specialists. As the need for revision arises, new individual pages will be published to supplant the original ones. The preparation of the new list is under the guidance of a checklist committee. The chairman and editor is William J. Riemer, Florida State Museum, Flint Hall, University of Florida, Gainesville.

Philip W. Smith
Retiring Chairman
ASIH Checklist Committee

A Morphological Section of the American Society of Zoologists was organized at the recent New York meeting of the AAAS. The aim of this new organization is to foster interest in comparative anatomy, one of the foundation stones of evolutionary theory. Officers of the Morphological Section are: *Chairman*, D. Dwight Davis, Chicago Natural History Museum; *Vice-chairman*, Harvey I. Fisher, Southern Illinois University; *Secretary*, Howard E. Evans, Cornell University.

INFORMATION FOR CONTRIBUTORS

Contributions to EVOLUTION may be in the fields of genetics, cytology, plant and animal taxonomy, paleontology, ecology, anthropology, bacteriology, or any other field of biology, provided that the facts and conclusions presented are of primary interest to the student of evolution. Descriptive material shall be included only so far as it is the basis of the evolutionary conclusions. Manuscripts are examined for suitability by members of the Editorial Board or other competent critics.

The length of manuscripts will be limited to twenty printed pages unless an exception is granted by the Editorial Board. Short manuscripts and discussions will be included in a separate section, "Notes and Comments." Half tones and tabular material will have to be kept within economic limits.

Proof should be corrected immediately on receipt, and returned at once with manuscript to the Managing Editor. Authors should leave forwarding directions whenever they move away from the address sent with the manuscript. Ordinarily page proof will not be sent to the author. Costs of changes in proof from the original copy will be charged to the author.

Reprints should be ordered when galley proof is returned. There is usually a delay of several weeks after publication before the author receives the reprints ordered. Illustrations and cuts will be destroyed, unless their return is requested on the reprint order.

Manuscripts should be typewritten in double spacing with ample margins and on only one side of the paper. The Editor should have *one carbon copy in addition* to the original manuscript. The author should keep one carbon copy.

Tables and captions for figures should be typed on separate sheets from the text. The legends for several figures may be placed on a single sheet.

Illustrations, including maps, should be referred to as "figures" wherever possible. Plates are reserved for illustrations that require paper inserts or for collections of small figures. All figures and plates are reduced to a maximum of 4⅜ inches in width and 6⅝ inches in length. Reductions may be stated in the caption but not on the figure.

All references to literature should be collected into a list of "Literature Cited" at the end of the article. See recent numbers of EVOLUTION for accepted style.

Titles should be short, preferably less than seven words. Footnote material should be incorporated in the text whenever possible.

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Manuscripts should be addressed to

I. Michael Lerner
Department of Genetics
University of California
Berkeley 4, California

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